

Hominin distribution and density patterns in Pleistocene China: Climatic influences[☆]



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ABSTRACT

At the broad Early/Middle/Late Pleistocene level, the Chinese hominin fossil site distribution data may inform on hominin mobility/behavioral/interaction strategies. Hominins during the Early Pleistocene and well into the Middle Pleistocene appear to be more restricted to central and southern China. By the advent of the late Middle Pleistocene hominins are found regularly in northern China and by the Late Pleistocene, hominin fossils are found in all latitudes and longitudes encompassing modern day China, and beginning some time during marine isotope stage 3 appear in higher altitudinal regions (e.g., Qinghai-Tibetan Plateau) as well. During the Middle Pleistocene a number of sites are found well away from major riverways suggesting an ability to transport potable water or perhaps an ability to be able to locate smaller bodies of fresh water. Given the paucity of evidence for storage containers until relatively recently in time, it is perhaps not that surprising that many of the Middle Pleistocene open-air sites are reportedly found in or near lacustrine environments. Hominins had a more restricted range due to climatic variation during the Early and early Middle Pleistocene, but were able to more successfully adapt to changing climates beginning during the late Middle Pleistocene. In part, this is due to a range of behavioral changes that hominins developed during the Pleistocene.

1. Introduction

“[S]ignificant events in human origins tended to occur during lengthy eras of strong climatic fluctuation” (Potts, 2012: 151).

For almost the entire Cenozoic, mammalian, including primate (Jablonski, 2005; Takai et al., 2014), evolution has been strongly impacted by paleoenvironmental changes (Janis, 1993). For instance, during the Miocene when major dessication events occurred (e.g., the Messinian Event) hominoids became less diverse while Old World monkeys became much more widespread, as the latter taxa were better able to adapt to the less forested environments. Jablonski (2005: 121) justifiably explains the reason for this as monkeys developed “a pattern of somewhat faster life histories, an ability to survive on eclectic, often low-quality diets, and the retention of an unspecialized quadrupedal locomotor habitus” (see also especially Jablonski et al., 2000). At some point during the Quaternary hominin populations became less susceptible to the whims of paleoenvironmental fluctuations. This was likely

related to biological changes, behavioral developments, or some combination of the two. Although never quite following a more monkey-like development, vis-à-vis the great apes, hominins, particularly beginning with *Homo erectus* were much better at adapting to changing environments. For instance, a plethora of evidence indicates that not only did *H. erectus* fall within the range of overall modern human body size for the first time in hominin evolution, they substantially increased their home ranges as well (Shipman and Walker, 1989; Walker and Leakey, 1993; Anton et al., 2002; Anton, 2007). This in turn, facilitated their much wider ranging dispersals than any of the other non-human primates, both monkeys and great apes alike, ever have achieved.

Based on current evidence, the earliest hominin to have successfully dispersed from Africa and into Asia was *Homo erectus*. Currently, the oldest *H. erectus* fossils to be identified in Asia are from Dmanisi in Georgia securely dated to between 1.85 Ma and 1.77 Ma (Gabunia et al., 2000; Lordkipanidze et al., 2013). In eastern Asia, *H. erectus* fossils have been dated in Indonesia from 1.6 Ma to as recently as

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143 ka (Anton and Swisher, 2004; Indriati et al., 2011; but see Kaifu, 2017), to 1.6 Ma at Gongwangling in central China (Zhu et al., 2015; but see An and Ho, 1989), and perhaps ~1.9–2.0 Ma at Mohui Cave, based on faunal correlations with the Early Pleistocene southern Chinese sites of Longgupo and Liucheng (Wang et al., 2005; Wang et al., 2007), and 1.7 Ma at Yuanmou (Zhu et al., 2008; but see Bae, 2010) in southern China. Reports of early Early Pleistocene hominin occupations are also present at Majuangou, Xiaochangliang, and Donggutuo in the Nihewan Basin, northern China starting at 1.66 Ma (Zhu et al., 2001, 2004). Although systematic fieldwork in the Nihewan Basin has been conducted for much of the past half century, with the discovery of thousands of lithic artifacts and tens of thousands of vertebrate fossils, it should be noted that hominin fossils have yet to be reported from these Early Pleistocene deposits. This is despite the fact that late Middle Pleistocene sites (e.g., Xujiayao) from the western side of the same basin has resulted in the discovery of numerous mid-Pleistocene *Homo* fossils (Norton and Gao, 2008a; Bae, 2010; Xing et al., 2015).

In all likelihood, there were many dispersal events from Africa to Asia during the Quaternary that involved multiple hominin taxa (minimally *H. erectus* and modern *H. sapiens*, and perhaps *H. heidelbergensis* and/or mid-Pleistocene *Homo*) (Templeton, 2002; Anton and Swisher, 2004; Rightmire, 2008; Klein, 2009; Bae, 2010; Conroy and Pontzer, 2012; Bae et al., 2017a, 2017b). However, hominins dispersing into Asia were moving into a landscape that was quite distinct from sub-Saharan Africa. Importantly, all discussion of hominin adaptability and survival in Asia must necessarily account for this broader environmental context. For instance, the earliest hominin dispersals out of Africa and into Asia that occurred some time during the Early Pleistocene and even later dispersals by modern humans from Africa to Asia during the Late Pleistocene were heavily influenced by geographic and environmental factors (Anton, 2007; Dennell, 2009, 2017). These influences included, but were obviously not restricted to, major geographic barriers (or at times, corridors) like the orogeny of the Himalayan mountain range and the Qinghai-Tibetan Plateau, to some degree the Qinling mountain range, major riverways like the Indus, Irrawaddy, Yellow, and Yangtze Rivers, to paleobathymetric variations that at times would have formed larger landmasses and at others smaller isolated island chains (Anton, 2007; Dennell, 2009, 2017; Norton and Jin, 2009; Norton et al., 2010a, 2010b; Boivin et al., 2013; Groucutt et al., 2015; Bae, 2017; Bae et al., 2017a, 2017b; O'Connor et al., 2017; Nakazawa and Bae, In press). It may even be possible that isolated natural geological events like the Toba super eruption some 74 ka in Indonesia could have caused regional and possibly even global die offs or bottlenecks of various faunas, including possibly early modern humans and other hominin populations (Rampino and Self, 1992; Ambrose, 1998). Growing evidence suggests however that, though considered a super eruption, the Toba explosion likely did not cause the catastrophic changes and hominin extinctions or bottlenecks as originally proposed (Petruglia et al., 2007, 2012; Roberts et al., 2015).

Given that hominins were moving into new environments and climate change clearly served to cause habitat loss and fragmentation throughout prehistory as it does today, early hominins were faced with a number of limited choices ranging from adaptation to extinction (Potts, 2012; Norton et al., 2010a; Beeton et al., 2014; Dennell, 2013, 2017; Glantz et al., 2018). For instance, during glacial periods, organisms are often forced to disperse to more habitable environs or concentrate in smaller geographic pockets or refugia [or simply “bottlenecks” (Bennett and Provan, 2008)]. With the possibility of extinction on the horizon, organisms are faced with several decisions to make. For example, would it be better to emigrate to different environs or become more concentrated in smaller refugia? Further, how can whatever the decision was be identified in the stratigraphic profile? Recent modeling of the Paleolithic record of Central Asia has been shedding potential light on the nature of these refugia, dispersal corridors, and perhaps eventual extinctions of individual groups. Importantly, these modeling

studies found that Central Asia may not have been as hostile during glacial periods as originally perceived and that certain areas, such as the foothills of the Tian Shan Mountains or more generally, the Inner Asian Mountain Corridor may have served as refugia (Beeton et al., 2014; Glantz et al., 2018). It may be possible that these regions served as natural ecotones where hominins would have been able to utilize resources from a wider diversity of environments.

It may be possible however that concentrating into smaller refugia like foothills was not possible and that in fact local extinctions occurred regularly. In examining the argument for Neanderthal survival/extinction probabilities in Europe during the Late Pleistocene, Hublin and Roebroeks (2009: 505–506) concluded that “[i]t is therefore unlikely that refuge zones could have accommodated sizable intrusive groups [of Neanderthals] during periods of climatic deterioration that caused depopulation of northwestern Europe... the periodic reduction of available areas could have instead led to an alternation of periods of extinction of northern populations and recolonisation of the northern areas by populations from the south.” If this is the case, re-populations of these regions during interstadials would have been by new populations and not simply the original populations expanding back out of these refugia when climatic conditions improved (see Hublin and Roebroeks, 2009; Dennell et al., 2011 for discussion). Indeed, this could be a plausible explanation for a complicated site like Denisova cave that has the fossil remains of Denisovans and Neanderthals in association with behavioral traces (e.g., perforated teeth, shell, stones, bone needles) that represent modern human behaviors that have long been considered to fall specifically within the realm of modern humans. In the case of Denisova, it is quite possible local extinctions followed by subsequent occupation by a completely new population occurred at least several times during the site's occupational history (Green et al., 2010; Reich et al., 2010; Bae et al., 2017a, 2017b).

Although complicated sites like Denisova where different hominin populations may have occupied during a relatively short time span have yet to be clearly identified further east, a more detailed study of the hominin fossil site distributions may contribute to a better understanding of what occurred in eastern Asia. Here, we present Pleistocene hominin fossil site data for China plotted on a series of topographic maps, given that simple maps may serve to obscure important information relevant for dispersal/occupation patterns in the region (Dennell, 2017). Although regions like Indonesia have extensive remains of *H. erectus* fossils (Kaifu et al., 2008) and places like Japan (Kaifu and Fujita, 2012; Nakazawa, 2017), Korea (Norton, 2000; Bae, 2010, 2014), and some areas of Southeast Asia [e.g., Tam Pa Ling (Demeter et al., 2012); Callao (Mijares et al., 2010); Lida Ajer (Westaway et al., 2017)] have reported early modern human fossils, the Chinese hominin paleontological record is the best known in Asia, rivaling many areas of Africa and Europe (Table 1; Wu and Wu, 1985; Pope, 1992; Wu and Poirier, 1995; Etler, 1996; Bae, 2010; Liu et al., 2014; Bae et al., 2017a). Further, studies of non-human primate distributions across Quaternary China already exist that have served to lay the groundwork for this further discussion of the nature of interactions between hominins and climate variation (e.g., Jablonski et al., 2000).

2. Quaternary hominin fossil distributions across China

Studies of non-human primates have shown that depending on their lifeways they may be more susceptible to the whims of climatic fluctuations (Jablonski, 2005; Takai et al., 2014). For instance, a growing number of studies have focused on the now extinct *Gigantopithecus* taxon, partially because it is the last known hominoid to have gone extinct (~300 ka: Rink et al., 2008) and because numerous suggestions have been forwarded that *Gigantopithecus* was the ancestor of the Yeti, Big Foot, and Sasquatch myths (Ciochon et al., 1990; Zhang and Harrison, 2017). Isotopic studies reconstructing *Gigantopithecus* diet indicates that they survived on a broad based C3 diet of fruits and leaves, stems, and perhaps hard tubers, but not a specialist of bamboo

Table 1
Pleistocene hominin fossil sites from China with basic descriptive data.

Site name	Taxa	Locations	Latitude	Longitude	Elevation(m)	Context	Age (ka)	Dating method	Reference ^a
Jianshi-Longgu Cave	Early Pleistocene <i>Homo erectus</i>	Jianshi County, Hubei	30° 39' 14.9" N	110° 04' 29.1" E	738	Cave	1800–2420	Magnetostratigraphic	Zheng, 2004
Lantian-Gongwangling	Early Pleistocene <i>Homo erectus</i>	Lantian County, Shaanxi	34° 11' N	109° 29' E	728	Loess	1150/1630	Magnetostratigraphic	An and Ho, 1989; Zhu et al., 2015
Meipu-Longgu Cave	Early Pleistocene <i>Homo erectus</i>	Yunxian County, Hubei	33° 0' 17" N	111° 10' 15" E	240	Cave			
Mohui cave	Early Pleistocene <i>Homo erectus</i>	Tiandong County, Guangxi	23° 34.89' N	107° 00.13' E	215	Cave			
Yuanmou-Danawu	Early Pleistocene <i>Homo erectus</i>	Yuanmou County, Yunnan	25° 45' N	101° 55' E		fluvial and alluvial silty clays	1700	Magnetostratigraphic	Zhu et al., 2008
Yuanmou-Guojiabao	Early Pleistocene <i>Homo erectus</i>	Yuanmou County, Yunnan	25° 40' N	101° 55' E		fluvial and alluvial silty clays			
Bailong Cave	Middle Pleistocene <i>Homo erectus</i>	Yunxi County, Hubei	32° 59' 40.0" N	110° 31' 33.6" E	550	cave			
Hexian-Longtan Cave	Middle Pleistocene <i>Homo erectus</i>	Hexian County, Anhui	31° 45' N	118° 20' E	23	cave	412 ± 25	U-series, ESR	Grün et al., 1998
Hualong Cave	Middle Pleistocene <i>Homo erectus</i>	Dongzhi County, Anhui	30° 06' 22.2" N	117° 1' 13" E		cave			
Hulu Cave	Middle Pleistocene <i>Homo erectus</i>	Nanjing City, Jiangsu	32° 03' 49.1" N	119° 02' 43.3" E		cave	239–620	U-series, ESR	Zhao et al., 2001
Lantian-Chenjiawo	Middle Pleistocene <i>Homo erectus</i>	Lantian County, Shaanxi	34° 13' 05" N	109° 15' 07" E		Loess	650	Magnetostratigraphic	An and Ho, 1989
Luonan	Middle Pleistocene <i>Homo erectus</i>	Luonan County, Shaanxi	34° 06' N	110° 08' E	950				
Nanzhao	Middle Pleistocene <i>Homo erectus</i>	Nanzhao County, Henan	33° 28' N	112° 41' E	265	cave			
Xichuan	Middle Pleistocene <i>Homo erectus</i>	Xichuan County, Henan	33° 09' N	110° 29' E					
Xuetangliangzi	Middle Pleistocene <i>Homo erectus</i>	Yunxian County, Hubei	31° 51' N	110° 38' E	200	fluvial and alluvial cave	830–870/581	Magnetostratigraphic, ESR	Li and Elert, 1992; Chen et al., 1997
Yanhui cave	Middle Pleistocene <i>Homo erectus</i>	Tongzi County, Guizhou	28° 15' N	113° 35' E		cave	113–181/206–240	U-series	Yuan et al., 1986; Shen and Linhong, 1991
Yiyuan	Middle Pleistocene <i>Homo erectus</i>	Yiyuan County, Shandong	36° 12' N	118° 9' E		cave			
Zhoukoudian Locality 1	Middle Pleistocene <i>Homo erectus</i>	Fangshan, Beijing	39° 41' N	115° 50' E	150	cave	200–770	U-series, ²⁶ Al/ ¹⁰ Be	Chen and Zhou, 2009; Shen et al., 2001a, 2001b, 2009
Changyang-Longdong Cave	mid-Pleistocene <i>Homo erectus</i>	Changyang County, Hubei	30° 15' N	110° 50' E	620	cave	195	U-series	Yuan et al., 1986
Chaoxian-Yinshan	mid-Pleistocene <i>Homo erectus</i>	Chaoxian County, Anhui	31° 33' N	117° 52' E		cave	200–160, 212/310–360	U-series	Chen et al., 1987; Shen et al., 2010
Dali-Tanshuigou	mid-Pleistocene <i>Homo erectus</i>	Dali County, Shaanxi	34° 52' N	109° 40' E		fluvial and alluvial cave	180–350	U-series, ESR	Yin et al., 2011
Jinniushan Lingjing	mid-Pleistocene <i>Homo erectus</i>	Yingkou City, Liangning Xuchang County, Henan	40° 34' 40" N 34° 04' N	122° 26' 38" E 113° 41' E	70 117	cave	190–310	U-series, ESR	Chen et al., 1994
Maba-Shizishan Cave	mid-Pleistocene <i>Homo erectus</i>	Qujiang County, Guangdong	24° 41' N	113° 35' E	85	alluvial cave	129/230–278	U-series	Li et al., 2017, 2017a
Mawokou Cave	mid-Pleistocene <i>Homo erectus</i>	Bingjie County, Guizhou	27° 43' 22.6" N	105° 22' 16.3" E		cave	112–178	U-series	Yuan et al., 1986; Shen et al., 2014
Miaohoushan	mid-Pleistocene <i>Homo erectus</i>	Benxi Man Autonomous County, Liangning	41° 13' 56" N	124° 07' 42" E	325	cave	200–500	U-series	Zhao et al., 2016

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Table 1 (continued)

Site name	Taxa	Locations	Latitude	Longitude	Elevation(m)	Context	Age (ka)	Dating method	Reference ^a
Panxian Dadong Cave	mid-Pleistocene <i>Homo</i>	Panxian County, Guizhou	25° 37' 38" N	104° 8' 44" E	1185	cave	130–300	U-series, ESR	Shen et al., 1997; Rink et al., 2003
Shigou	mid-Pleistocene <i>Homo</i>	Xiangfen County, Shanxi	35° 45.9' N	111° 25.3' E		fluvial and alluvial			Du et al., 2014
Xinglong Cave Xujiaiyao	mid-Pleistocene <i>Homo</i> mid-Pleistocene <i>Homo</i>	Fengjie County, Chongqing Yangyuan County, Hebei	30° 37' 39" N 40° 06' 02" N	109° 08' 06" E 113° 58' 39" E	980	cave	120–150 160–200	U-series OSL	Gao et al., 2004 Li et al., 2014
Zhoukoudian Locality 4 Dingmo Cave	mid-Pleistocene <i>Homo</i> early Late Pleistocene early modern humans	Fangshan District, Beijing Tiaodong County, Guangxi	39° 41' N 23° 36' N	115° 50' E 106° 59' E	150 140	cave	248–269	U-series	Shen et al., 2004
Fuyan Cave	early Late Pleistocene early modern humans	Daoxian County, Hunan	25° 39' 02.7" N	111° 28' 49.2" E	232	cave	80–120	U-series	Liu et al., 2015
Huanglong	early Late Pleistocene early modern humans	Huanglong County, Shaanxi	35° 35' N	109° 52' E		cave			
Huanglong Cave	early Late Pleistocene early modern humans	Yunxi County, Hubei	33° 07' N	110° 13' 04.3" E	601	cave	81–101	U-series	Shen et al., 2013
Liujiang-Tongtianyan Cave	early Late Pleistocene early modern humans	Liujiang County, Guangxi	24° 10' 59" N	109° 25' 56" E		cave	111–139	U-series	Shen et al., 2002
Longdong Cave	early Late Pleistocene early modern humans	Longlin Ge Autonomous County, Guangxi	24° 54' N	105° 17' E	1200	cave			
Luna Cave in Bubing	early Late Pleistocene early modern humans	Tiaodong County, Guangxi	23° 36' 48" N	106° 58' 1" E		cave	70–127	U-series	Bae et al., 2014
Zhiren Cave (<i>Homo sapiens</i> Cave)	early Late Pleistocene early modern humans	Chongzuo City, Guangxi	22° 17' 13.6" N	107° 30' 45.1" E	179	cave	100–113	U-series	Liu et al., 2010a, 2010b
Dingcun	early Late Pleistocene modern humans	Xiangfen County, Shanxi	35° 49' N	111° 25' E	410	fluvial and alluvial	75–114	U-series	Chen et al., 1984
Xianren Cave	early Late Pleistocene modern humans	Xichou County, Yunnan	23° 26' N	104° 42' E		cave	47–105	U-series	Zhang et al., 2004
Bailian Cave	late Late Pleistocene modern humans	Liuzhou City, Guangxi	24° 12' 54" N	109° 25' 37" E	249	cave	33	AMS	Zhou, 2007
Baojiyan Cave	late Late Pleistocene modern humans	Gulin City, Guangxi	25° 17' 20.7" N	110° 17' 58.0" E		cave			
Changwu	late Late Pleistocene modern humans	Changwu County, Shaanxi	35° 14' 57.1" N	107° 47' 56.4" E					
Cho-chen	late Late Pleistocene modern humans	Tainan City, Taiwan	23° 03' 51.7" N	120° 23' 21.0" E			20–30	AMS	Shikama et al., 2008
Chuandong Cave	late Late Pleistocene modern humans	Puding County, Guizhou	28° 18' N	105° 45' E	1264	cave	12	AMS	Zhao et al., 2017
Duan-R5013	late Late Pleistocene modern humans	Duan Yao Autonomous County, Guangxi	23° 59' N	108° 00' E		cave			
Ganqian Cave	late Late Pleistocene modern humans	Liujiang County, Guangxi	24° 13' 22" N	109° 05' 14" E	160	cave	85–139	U-series	Shen et al., 2001a, 2001b
Gezi Cave	late Late Pleistocene modern humans	Chaoyang City, Liangning	41° 17' 36" N	119° 58' 37" E		cave			
Gutougou	late Late Pleistocene modern humans	Wushan County, Gansu	34° 47' N	104° 40' E		cave	41–43	¹⁴ C	Xie et al., 1987
Huli Cave	late Late Pleistocene modern humans	Qingliu County, Fujian	26° 02' N	117° 03' E		cave			
Jiande	late Late Pleistocene modern humans	Jiande City, Zhejiang	29° 22' 53.7" N	119° 02' 07.4" E		cave			
Jianping	late Late Pleistocene modern humans	Jianping County, Liangning	41° 54' 18.0" N	119° 42' 55.0" E		cave			
Jimuyan Cave	late Late Pleistocene modern humans	Pingle County, Guangxi	24° 29' 52.8" N	110° 5' 0.79" E	163	cave			

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Table 1 (continued)

Site name	Taxa	Locations	Latitude	Longitude	Elevation(m)	Context	Age (ka)	Dating method	Reference ^a
Laoya Cave	late Late Pleistocene modern humans	Bijie County, Guizhou	27° 21' 12.57" N	105° 1' 8.46" E		cave	21–24	AMS	Xing et al., 2017
Lijiang	late Late Pleistocene modern humans	Lijiang City, Yunnan	26° 47' N	100° 17' E					
Longtanshan Cave 1	late Late Pleistocene modern humans	Chengong County, Yunnan	24° 49' N	102° 49' E	1940	cave	20–80	U-series	Gao et al., 2007
Longtanshan Cave 2	late Late Pleistocene modern humans	Chengong County, Yunnan	24° 49' N	102° 49' E	1940	cave	31–33	¹⁴ C	Qiu et al., 1985
Malu Cave	late Late Pleistocene modern humans	Mengzi City, Yunnan	23° 20' N	103° 24' E		cave	13–14	AMS	Curnoe et al., 2012
Maomao Cave	late Late Pleistocene modern humans	Xingyi County, Guizhou	25° 31' N	105° 01' E	1310	cave	13.3–15.7	U-series	Yuan et al., 1986
Miaohoushan-East Cave	late Late Pleistocene modern humans	Benxi Man Autonomous County, Liangning	41° 13' 56" N	124° 07' 42" E	350	cave	32	¹⁴ C	Liaoning Museum and Benxi Museum, 1986
Nalái Cave	late Late Pleistocene modern humans	Longlin Ge Autonomous County, Guangxi	24° 53' 11" N	105° 7' 42" E		cave			
Nanshan Cave	late Late Pleistocene modern humans	Fusui County, Guangxi	22° 23' 24" N	107° 33' 41" E	140	cave	30–40	U-series	Wang and Mo, 2004
Niujiaogou	late Late Pleistocene modern humans	Jingchuan County, Gansu	35° 23' N	107° 28' E			15–48	OSL	Li et al., 2010
Qianyang Cave	late Late Pleistocene modern humans	Donggang City, Liangning	40° 05' N	124° 11' E	90	cave	16–22	U-series	Fu et al., 2008
Qilishan	late Late Pleistocene modern humans	Laibin City, Guangxi	23° 45' N	109° 05' E		cave	38.5–44	U-series	Shen et al., 2007
Shuidonggou	late Late Pleistocene modern humans	Lingwu City, Ningxia	38° 21' N	106° 29' E	1200				
Shuiyan East Cave	late Late Pleistocene modern humans	Lipu County, Guangxi	24° 31' N	110° 24' E		cave			
Sjara-osso-gol (Salawusu) in Hetao	late Late Pleistocene modern humans	Erdos City, Inner Mongolia	37° 10' 59" N	108° 10' 58" E	1300	fluvial and alluvial cave	44–125/0.22	TL, ²³⁰ Th, IRSL, AMS	Shang et al., 2006; Keates et al., 2007
Tianyuan Cave	late Late Pleistocene modern humans	Fangshan District, Beijing	39° 39' 28" N	115° 52' 17" E	175		40	AMS	Shang et al., 2007
Upper Cave	late Late Pleistocene modern humans	Fangshan District, Beijing	39° 41' N	115° 50' E	170	cave	33–45	AMS	Li et al., n.d.
Wuzhutai	late Late Pleistocene modern humans	Xintai City, Shandong	35° 83' N	117° 70' E					
Yaner Cave	late Late Pleistocene modern humans	Shimen County, Hunan	29° 41' 30.8" N	111° 14' 43.3" E		cave	14		
Zhaotong	late Late Pleistocene modern humans	Zhaotong City, Yunnan	27° 30' N	103° 48' E		cave			
Ziyang	late Late Pleistocene modern humans	Ziyang County, Sichuan	30° 07' N	104° 39' E		fluvial and alluvial	30	¹⁴ C	

^a Some data are not available for all of these sites (as indicated by the blank cells). For sites that do not have a citation, please refer to Liu et al. (2014).

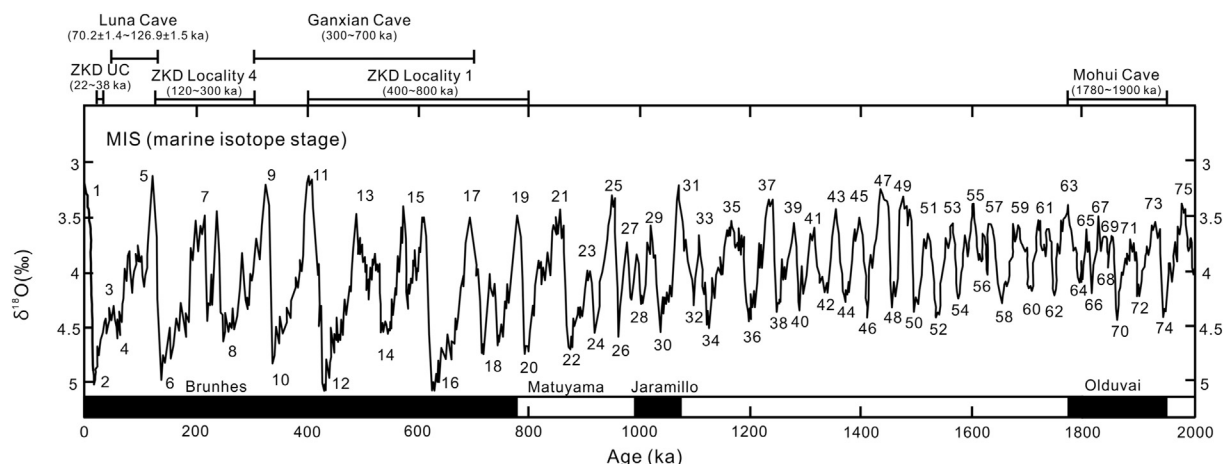


Fig. 1. Paleoclimate and marine isotope stages across the Quaternary. The marine isotope stages for primary sites mentioned in the text are presented here. Redrawn after Lisiecki and Raymo (2005: their Fig. 4).

as earlier suggested (Nelson, 2014; Bocherens et al., 2017). Its diet breadth was broader than *Sivapithecus*, a Miocene ape thought to have been on the same lineage as *Gigantopithecus* that eventually gave rise to extant *Pongo*. *Gigantopithecus* is thought to have lived in a “humid subtropical densely vegetated forest with a continuous canopy” (Zhang and Harrison, 2017: 169). Although more flexible in terms of their overall diet breadth compared to *Sivapithecus*, *Gigantopithecus* was not capable of surviving in more open grassland environments during glacial periods as suggested by the paucity of C4 plants in its diet (Bocherens et al., 2017). This, along with an overall estimated slower reproductive cycle in line with extant *Pongo* is thought to have contributed to the eventual extinction of *Gigantopithecus* (Jablonski et al., 2000; Zhang and Harrison, 2017).

In order to develop a better understanding of primate distribution variation in light of environmental fluctuations, Jablonski et al. (2000) evaluated site distributions of *Pongo*, *Hylobates*, Cercopithecidae, and Hominidae across China during the Pleistocene. In their study they found that *Pongo* and *Hylobates* distributions were more restricted by changing environments, cercopithecids less so, and hominins the least, particularly when moving from the Early Pleistocene to the Late Pleistocene. Given the relationship between *Gigantopithecus* and *Pongo* it is perhaps not that surprising that the former taxon was restricted to a small region of southern China and perhaps northern Thailand and northern Vietnam (Zhang and Harrison, 2017). Directly relevant to the current study however, one of the primary conclusions Jablonski et al. (2000: 154) drew was that “[t]he ecological association of hominids with other catarrhines was strong in the Early Pleistocene, but became weaker through time as culture permitted hominid range expansion into habitats off limits to other catarrhines for most of the year.” It may be possible that this ecological association extended to some degree into the Middle Pleistocene. For instance, macaques have been found in Middle Pleistocene deposits in northern China and Korea and obviously, are still present in the Japanese archipelago, though proposed to have arrived there initially some time during MIS 12 (Iwamoto and Hasegawa, 1972; Jablonski et al., 2000; Norton, 2000; Norton et al., 2010a; Nakazawa and Bae, in press). This dispersal appears to follow the general global warming trend during the Middle Pleistocene as typical warm and wet adapted faunas like *Bubalus* have also been identified in northern China as well (Han and Xu, 1985; Norton et al., 2010a).

Having more robust up-to-date hominin fossil data available to us, we asked whether the same pattern in hominin site occupation is still present. In order to develop a general idea of hominin occupation patterning in eastern Asia during the Pleistocene we evaluated the best known record, that from China. We mapped Early and Middle Pleistocene *Homo erectus*, late Middle Pleistocene mid-Pleistocene *Homo*

(aka “archaic *Homo sapiens*”), and Late Pleistocene modern *H. sapiens* (Figs. 2–6). Given the importance of testing the single dispersal Out of Africa at 60 ka model (Bae et al., 2017a, 2017b), we divided the Late Pleistocene modern human data into two separate maps with the division at 60 ka (Figs. 5–6). Here, we divide China up into North (anywhere north of the Yellow River and Qinghai Mountain Range), South (anywhere south of the Yangtze River), and Central (the region between the Yellow and Yangtze rivers). It should be noted that these regions tended to be fluid during the Pleistocene as warm adapted faunas would often be found further north during interglacials, cold adapted faunas present further south during glacials, and a mixture of Palearctic and Oriental taxa present in Central China. The near-absence of any geographic barrier east of the Qinghai Mountain Range would have facilitated these faunal and floral movements (Norton et al., 2010a).

There may be some variability between our dataset and the site database compiled by Jablonski et al. (2000) because of the addition of new hominin fossil sites reported since the late 1990s. Further, we restricted our evaluation to only sites where hominin fossils are reported. Thus, an Early Pleistocene site like Xihoudu where no hominin fossils have been found, but archaeology were reported, that appears in Jablonski et al.’s (2000) Fig. 1 Early Pleistocene Hominidae map was excluded from our study. Other sites, like Longgupo, that were tentatively considered a hominin fossil locality at the time of the Jablonski et al. (2000) publication, were excluded from this study given the taxonomic questions that still exist about the hominoid fossils from that site (Wu, 2000; Etlar et al., 2001). We realize the limitations of restricting our database to only hominin fossil localities, but given that the number of Paleolithic sites in China now numbers in the thousands and are of variable confidence, it is beyond the scope of the current study to evaluate all of these non-hominin bearing Paleolithic sites across time and space. When applicable however, we do mention a few non-hominin bearing archaeology sites that are relevant to this discussion.

In an ideal situation, we would be able to dig down further into this database by separating out sites or specific stratigraphic layers restricted to glacial periods from sites/layers assigned specifically to interglacial stages. For instance, Beeton et al. (2014) assigned Late Pleistocene sites from Central Asia to glacial or interglacial stage based primarily on cultural indicators. However, because many Chinese hominin sites, particularly the localities from the Early and Middle Pleistocene span both warm and cold marine isotope stages, we need to be careful in reading too much into occupation data without a clear understanding of the specific ages of occupations within these deposits. For instance, the current dating of Zhoukoudian Locality 1 is between ~780 ka – 400 ka (Shen et al., 2009), a time span that includes 5 glacial and 4 interglacial marine isotope stages (Fig. 1). Nevertheless, the

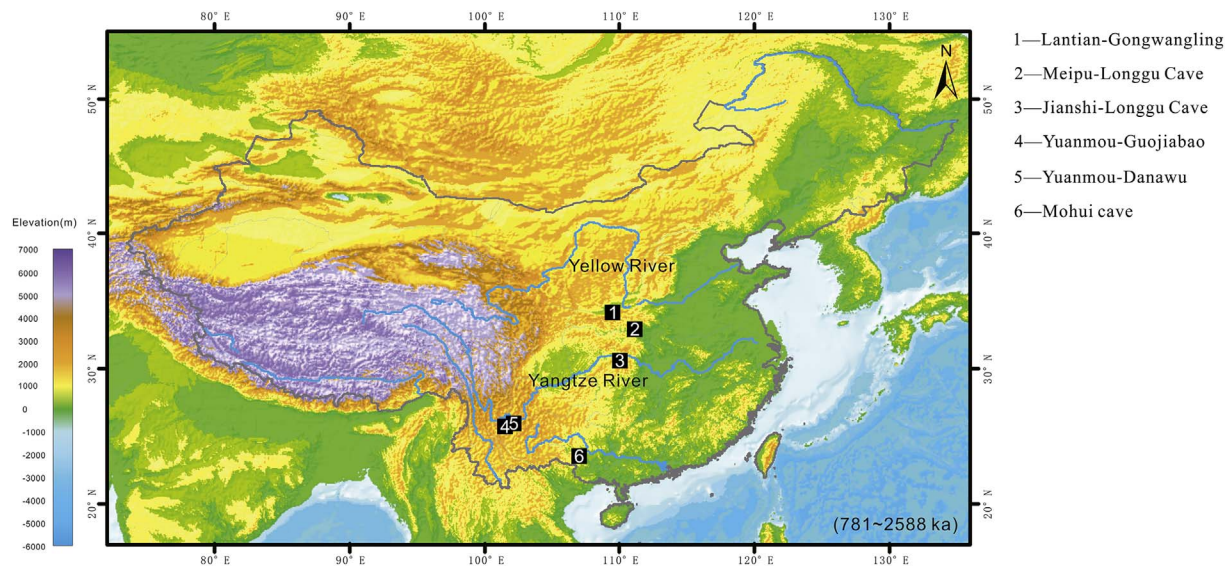


Fig. 2. Distribution of *Homo erectus* fossils in China during the Early Pleistocene. Elevation scale is presented on the left side of the topographic map.

Beeton et al. (2014; see also Glantz et al., 2018) study is an interesting methodological approach that should be investigated further if a more robust database can be developed.

The general observations we draw are that although the number of Early Pleistocene *H. erectus* sites is currently few in number, they are generally restricted to southern and central China (Fig. 2). Further, the sites are found specifically along major riverways. This may be a result of a greater number of field projects designed to investigate these major riverways rather than the more dense mountainous regions. However, it has long been postulated that Pleistocene hominins need regular access to potable water which would have restricted their movement somewhat without any way to store water (Groucutt et al., 2015; Bae et al., 2017a, 2017b; Dennell, 2017). Even the Lantian-Gongwangling site, found in loess deposits (Table 1), is relatively close to a major riverway. It is only when we move into the Middle Pleistocene where actual fossil evidence of *H. erectus* appears further north at sites like Zhoukoudian Locality 1 and further east at Yiyuan in Shandong Province (Fig. 3). Moreover, a number of *H. erectus* fossils have been found between the Yangtze and Yellow rivers, thus, suggesting a wider hominin dispersal when moving into the Middle Pleistocene. Given that many of these

Middle Pleistocene *H. erectus* open-air sites are actually located in lacustrine deposits (Table 1), it is clear that identification and proximity to potable water sources remained a critical constraint.

Of course, an absence of evidence is not necessarily evidence of absence. It should be remembered that this particular evaluation is restricted to sites that have hominin fossils and not necessarily archaeological sites that are generally accepted, but have no hominin fossils. For instance, as mentioned above, some of the earliest reported hominin presence in northern China is from the Nihewan Basin at ~1.6 Ma (Zhu et al., 2001, 2004). Nevertheless, none of these early sites have produced any evidence of actual hominin fossils. Based on this current dataset, it would appear that Chinese *H. erectus* was more restricted to the Oriental biogeographic zone and moved northward when the boundary line separating the Palearctic and Oriental biogeographic zones moved in that direction during the Middle Pleistocene (Norton et al., 2010a). This may be considered a bit unusual given that *H. erectus* are known from Dmanisi, an Early Pleistocene site in Georgia (Lordkipanidze et al., 2013), well geographically situated in the Palearctic biogeographic zone. The evidence from the Nihewan Basin may be considered anomalous as well as it is currently the only reported

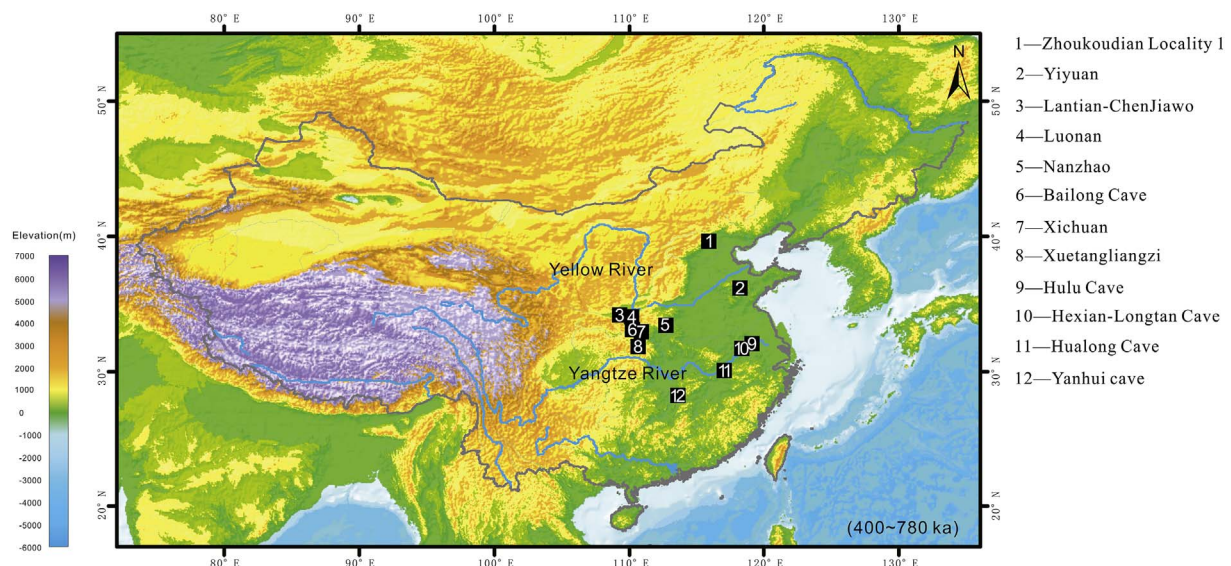


Fig. 3. Distribution of *Homo erectus* fossils in China during the Middle Pleistocene. Elevation scale is presented on the left side of the topographic map.

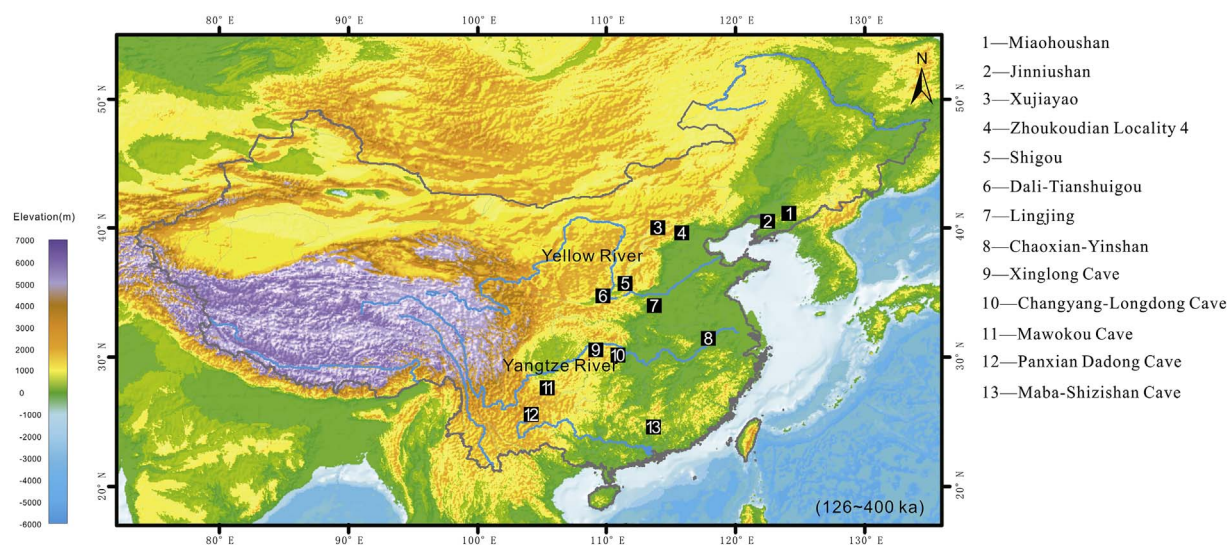


Fig. 4. Distribution of mid-Pleistocene *Homo* (aka “archaic” *Homo sapiens*) fossils in China. These generally are restricted to the late Middle Pleistocene. Elevation scale is presented on the left side of the topographic map.

evidence of hominin occupation in northern China during the Early Pleistocene.

Mid-Pleistocene *Homo*, though still relatively few in number, are found throughout China and as far north as Zhoukoudian Locality 4, Jinniushan, Miaohoushan, and Xujiayao and as far south as Maba (Fig. 4). This northward expansion may in part be related to the general warming trend experienced during the Middle Pleistocene and observed by many other vertebrate faunas, such as various non-human primates (Jablonski et al., 2000; Norton, 2000; Norton et al., 2010a). Although still not clear about Zhoukoudian Locality 1H. *erectus*’ ability to procure large game on a regular basis (Boaz et al., 2004), there is good evidence that late Middle Pleistocene hominins in northern China were able to regularly hunt large faunas successfully. The mid-Pleistocene *Homo* site of Xujiayao located northwest of Zhoukoudian, originally interpreted as a “horse-kill site” (Jia and Wei, 1976) and later verified by taphonomic studies (Norton and Gao, 2008a) is a case in point. Clearly, at some point during the Middle Pleistocene, hominins were able to better adapt to these more northerly climates in eastern Asia. Although the Middle Pleistocene was generally warmer than the Early or Late Pleistocene, it is still acknowledged that survival of the winter climes in the northern latitudes would have been difficult to impossible without the biological and/or cultural adaptations/developments in place. The ability to regularly procure large game can be seen as one such behavioral adaptation (Norton and Gao, 2008a; Norton and Jin, 2009).

Early modern humans appear in higher density during the early Late Pleistocene (120 ka–60 ka) in southern China, with pockets in central and north, while more recent modern humans dated to the late Late Pleistocene (60 ka – 10 ka) are found more evenly distributed throughout the geographic region (Figs. 5–6). As with the trend that began during the Middle Pleistocene, an increasing number of sites are located away from major waterways. In addition, particularly in the dense karst limestone mountainous areas of southwestern China, a number of modern human fossils have been found in cave deposits, a pattern that begins to appear during the Middle Pleistocene (Fig. 7). Interestingly, during the early Late Pleistocene early modern humans have been identified in higher density in southern China, which may lend some support for their initial appearance in the region following a southern dispersal route out of Africa (Bae et al., 2017a, 2017b). It should be noted however, that there is an absence of modern human fossils in northwestern China that have been dated to the early Late Pleistocene. In this particular case, this may be the result of fewer research programs active in Northwest China. However, field and laboratory initiatives in Central Asia (Glantz et al., 2018), southern

Siberia (Buzhilova et al., 2017), and Mongolia (Jaubert, 2015) have found little evidence of a modern human presence during the early Late Pleistocene. The findings from Denisova Cave of early modern human behavior aside (Derevianko and Rybin, 2003), a northern dispersal route out of Africa by modern humans was likely a later trek than the southern migration route (Bae et al., 2017a, 2017b). Further, the fact that a number of early Late Pleistocene sites [e.g., Luna, Zhiren, Huanglong, and perhaps Fuyan (Liu et al., 2010a, 2010b, 2015; Bae et al., 2014, 2017a; Michel et al., 2016)], all located in southern and central China, is suggestive of a southern dispersal out of Africa.

3. Discussion

It is not until well into the Middle Pleistocene where hominins become more widely distributed across China. It is possible that this could simply be a result of more extensive fieldwork being conducted in younger deposits. However, most paleoanthropologists would agree that *H. erectus* evolved in Africa and dispersed across Asia some time during the Early Pleistocene, but in relatively smaller groups. Thus, it may not be that surprising that fewer Early Pleistocene sites have been identified in China vis-à-vis Middle and Late Pleistocene localities. The key point here is the geographic distribution of these hominin fossil sites. By the advent of the Late Pleistocene, hominin fossils are found in all latitudes and longitudes encompassing modern day China and beginning some time during MIS 3 appear in higher altitudinal regions (e.g., Qinghai-Tibetan Plateau) as well. Beginning during the latter part of the Middle Pleistocene, a number of sites are found well away from major riverways suggesting an ability to transport potable water or perhaps an ability to be able to locate smaller bodies of fresh water. In fact, many Middle and Late Pleistocene open-air sites are actually found in lacustrine environments (Table 1).

Further, as a number of researchers have noted over the years, the ability of hominins to move into these novel environments was due primarily to behavioral changes which could occur within the span of a single generation, but as well as to physiological changes that normally take several generations to take effect (Moore et al., 1998; Beall, 2001; Aldenderfer and Zhang, 2004; Norton and Jin, 2009; Bae, 2017; Bae et al., 2017b). For instance, the presence of bone needles, long considered to be representative evidence for sewn clothing (Pei, 1939; Norton and Gao, 2008b; Norton and Jin, 2009), and indirect skeletal morphology such as gracile pedal phalanges (Trinkaus and Shang, 2008) are clear evidence that at some point during the Late Pleistocene humans were able to adapt to a range of different environments. Thus,

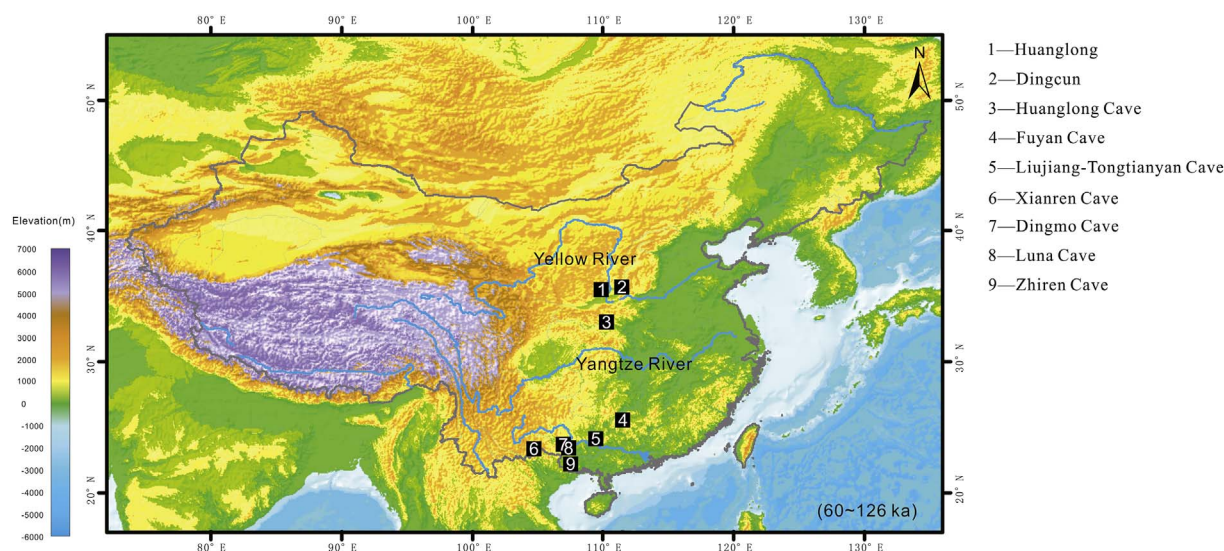


Fig. 5. Distribution of *Homo sapiens* fossils in China during the early Late Pleistocene (120 ka – 60 ka). Elevation scale is presented on the left side of the topographic map.

it is perhaps not that surprising that only when we begin to see major behavioral changes across the region that we see evidence that humans successfully traversed these novel terrains. For instance, data presented in Fig. 6 shows clearly that site occupation at higher altitudes (2000–1000 MASL) in China is a relatively recent phenomenon, with only one site dating prior to the Late Pleistocene (the late Middle Pleistocene Dadong cave site located in Guizhou) where hominin fossils have been reported (Table 1). Granted, not all of these sites have reported altitudes, but the pattern does seem to be consistent that the move into higher altitudes was a recent development. Indeed, excavation of sites that are at high altitudes (3000–4000 MASL), such as Heimahe and Jiangxigou postdate the Last Glacial Maximum and are considered to have been only short term camps (Madsen et al., 2006). In fact, it has been suggested that permanent occupation of these higher altitudinal regions could not have been possible until the advent of animal domestication in the region “which would have resulted in a reliable food and clothing source” (Norton and Jin, 2009: 253). Current evidence suggests permanent occupation of these high altitude regions occurred only around 6000 years ago (Aldenderfer and Zhang, 2004; Madsen et al., 2006).

More detailed evaluation of the occupational histories of sites that cross cut time and space should provide additional information

regarding whether certain regions may have served as refugia (Beeton et al., 2014; Dennell, 2017; Glantz et al., 2018). Indeed, Glantz et al. (2018: 91) postulated whether there is “something unique about the Inner Asian Mountain Corridor and greater central Asia, or are all foothill zones across the Old World important refugia for hominins during times of climatic instability?”. Based on the five distribution maps presented here for Pleistocene hominin fossil sites in China, the only site that continually reappears from the Middle Pleistocene onward is Zhoukoudian [Locality 1 (*H. erectus*), Locality 4 (mid-Pleistocene *Homo*), Upper Cave (*H. sapiens*)]. The question then becomes, should Zhoukoudian be considered one of these so-called refugia? Given that the hominin occupation of the various Zhoukoudian localities span some 800,000 years, it would be interesting to see if the hominin occupation data can be pinpointed, with any degree of confidence, to strictly glacial (suggestive of a refugium), interglacial (suggestive of an expansion out of a refugium), or both and what would that tell us about hominin movements in northern China from the Middle Pleistocene onward? In fact, review of the stratigraphic profiles and current dating sequences of these localities from Zhoukoudian suggest occupation during both glacial and interglacial periods. For instance, Upper Cave appears to now be securely dated to MIS 3, Locality 4 appears to be dated to MIS 5–8, and the various *H. erectus*

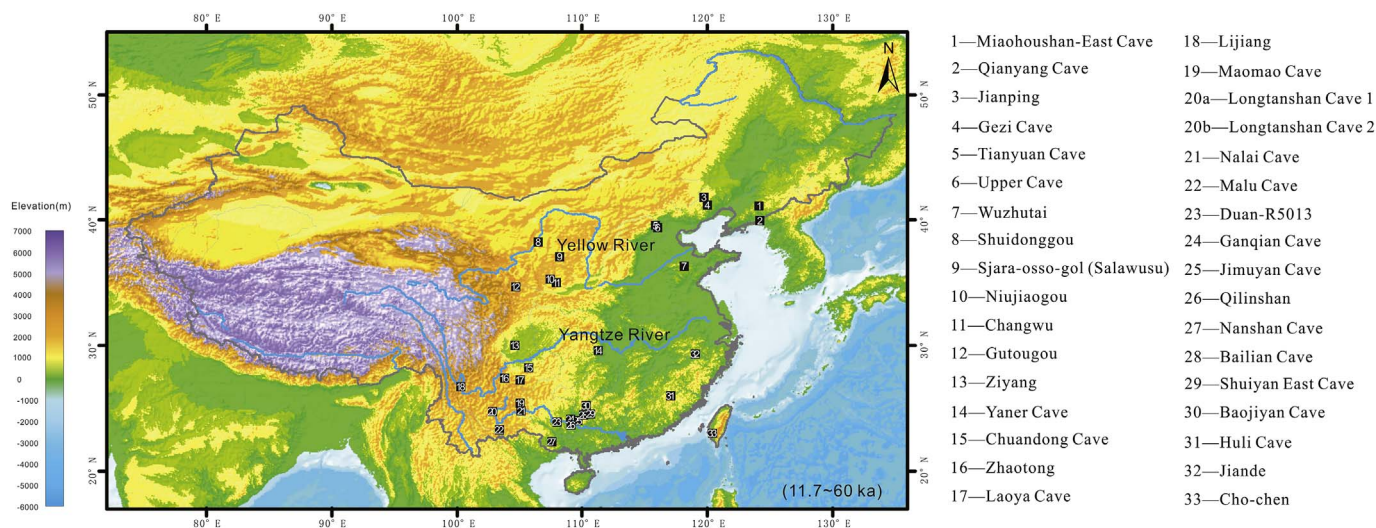


Fig. 6. Distribution of *Homo sapiens* fossils in China during the late Late Pleistocene (60 ka – 10 ka). Elevation scale is presented on the left side of the topographic map.

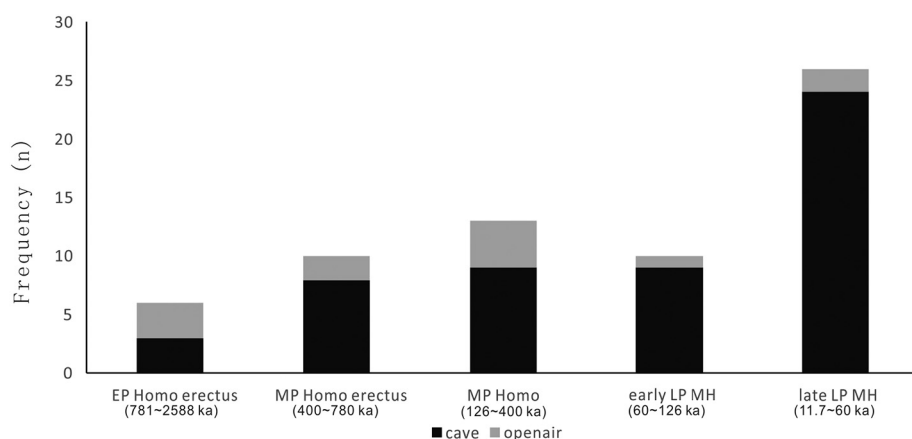


Fig. 7. Tabulated site data broken down by context (cave vs. open-air) and time period and hominin fossil group. EP *Homo erectus* = Early Pleistocene *Homo erectus*; MP *Homo erectus* = Middle Pleistocene *Homo erectus*; MP *Homo* = mid-Pleistocene *Homo*; early LP MH = early Late Pleistocene (120–60 ka) modern human; late LP MH = late Late Pleistocene (60–10 ka) modern human. Site data from Table 1.

crania from Locality 1 to MIS 11, 13, 15–18 (Shen et al., 2004, 2009; Li et al., In Press). Shen et al. (2004: 337) even concluded that their re-dating of Locality 4 supports “the hypothesis that human occupation of the Zhoukoudian sites has been more or less continuous over hundreds of thousand years.” Clearly, more detailed analyses are required to really determine how regularly these Zhoukoudian localities were occupied and for how long was each occupation episode. Particularly relevant is the fact that these sites were consistently abandoned by hominins on a regular basis as evidenced by the presence of multiple carnivore layers, particularly at Locality 1 (Boaz et al., 2004; Norton and Gao, 2008a, 2008b). However, if continually occupied localities appear in northern China, what of the case then for southern China that has yet to provide evidence of this type of continuous hominin presence at one locality or geographically restricted area such as a river basin?

Two areas of Guangxi, Bubing Basin and Chongzuo, may inform better on the situation in southern China. Over the past several decades, these two areas have provided a diversity of important paleoecological data, some linked to hominin dispersals/occupations (Wang et al., 2007; Liu et al., 2010a; Bae et al., 2014; Jin et al., 2014). Importantly, even in these fairly well researched areas we do not see a single area/site that has evidence of this type of continuous hominin occupation as in the case of the Zhoukoudian localities. Although *H. erectus* has been tentatively identified in Early Pleistocene Mohui Cave (Wang et al., 2005) and modern *H. sapiens* in nearby early Late Pleistocene Luna Cave (Bae et al., 2014), there is a long absence of additional hominin fossils from caves in the Bubing basin that date from the late Early Pleistocene and Middle Pleistocene. In the case of Chongzuo, currently only the hominin fossils from early Late Pleistocene Zhiren Cave have been well reported (Liu et al., 2010a), though Takai et al. (2014) mentions another Late Pleistocene locality Shuangtan Cave that may also have a few hominin fossils.

Nevertheless, because the paleontological data is fairly abundant from Bubing Basin and Chongzuo these data could at least inform on what the environment resembled during broad chunks of time. Broadly speaking, numerous studies have shown that a great deal of diversity is present in the faunal complex from the Bubing Basin that represents a variable environment (Chen et al., 2001; Shen et al., 2001a, b; Wang et al., 2007; Wang, 2009). Good examples may be evident from Chui-feng, Wuyun, and Lower Pubu caves. The paleontology from the Early Pleistocene Chui-feng cave site include tropical-subtropical forest elements such as *Tapirus*, *Gigantopithecus*, *Hylobates*, *Arctonyx*, *Rhinoceros*, *Muntiacus*, *Cervus* (*Rusa*), *Stegodon*, *Sinomastodon*, *Ailuropoda*, *Hesperotherium*, *Macaca*, *Ursus*, and *Sus*. Interestingly, *Equus*, a temperate grassland member, and *Pachyrocota*, a tropical-subtropical grassland taxon, were also identified in the Chui-feng deposits. The Chui-feng fauna is considered primarily an Oriental faunal complex with a few elements typical of the Palearctic biogeographic realm (Wang, 2009). The late Middle Pleistocene Wuyun Cave faunas are typical of the Oriental

Realm. Many of the taxa are present only in tropical/subtropical areas, such as *Felis pardus*, *Paradoxurus*, *Macaca*, *Presbytis*, *Pongo*, *Atherurus*, *Hystrix*, *Cervus*, *Elephas*, and *Rhinoceros*, while others are more widely distributed throughout Southeast Asia, such as *Cuon*, *Ursus*, and *Arctonyx*. The Wuyun fauna clearly represent a warmer more heavily forested environment during the late Middle Pleistocene (Chen et al., 2001). The late Late Pleistocene Lower Pubu Cave fauna is also dominated by tropical - subtropical elements, such as *Macaca*, *Hystrix*, *Rhizomys*, *Arctonyx*, *Ursus*, *Ailuropoda*, *Elephas*, *Megatapirus*, *Rhinoceros*, *Sus*, *Muntiacus*, and *Cervus*. However, the appearance of *Equus* indicates a climate that was much cooler than during the Middle Pleistocene or Holocene, and that grasslands must have been present in the basin during the last glacial period (Wang et al., 2007).

Thus, the presence of equids at the Early Pleistocene Chui-feng Cave and the late Late Pleistocene Lower Pubu Cave, but absent during the warmer and more humid Middle Pleistocene in the basin, clearly indicates variability in the climate (Wang et al., 2007; Norton et al., 2010a). These could be good examples of Palearctic faunas like equids being driven southward in the wake of increasingly hostile environments further north. Given the recent suggestion by Hublin and Roebroeks (2009) however that we may actually be observing local extinction events rather than temporary emigration episodes, further analyses are clearly warranted. Finding additional equid fossils from specific glacial deposits throughout the Bubing Basin and more broadly southern China would reinforce the argument that these Palearctic faunas were indeed driven southward during glacial advances and reflects a much drier environment. Presence/absence of other heavily climate-impacted faunas can also inform on the variability of the paleoenvironment. For instance, Lycett and Bae (2010) observed that *Rhizomys* (bamboo rat) was only present in North China at the Middle Pleistocene Zhoukoudian Locality 1 site, but absent in Early and Late Pleistocene deposits from the region. This indirect evidence was used to suggest that the extent of bamboo forests likely varied in northern China and probably was not continuously present throughout the Quaternary.

Further, clay mineral analyses of various sections from Mohui Cave (Early Pleistocene), Ganxian Cave (Middle Pleistocene), and Luna Cave (Late Pleistocene) in Bubing Basin shows clearly how the paleoclimate has constantly fluctuated in the basin over the past two million years (Fig. 8; Cheng, 2016; Huang, 2016). In each of the sections at least half of the profile represents colder dry conditions. The key will then be to be able to effectively link these clay mineral profiles to the paleontology and see if true Palearctic taxa (e.g., *Equus*) only appear during colder drier conditions and then disappear when the climate becomes warmer and wetter. Same could be applied with typical Oriental taxa (e.g., *Bubalus*, *Rhizomys*) appearing further north only in deposits where the clay mineral analyses indicates warmer wetter conditions. This combination of paleontology, clay mineral, and isotope studies (e.g., Wang

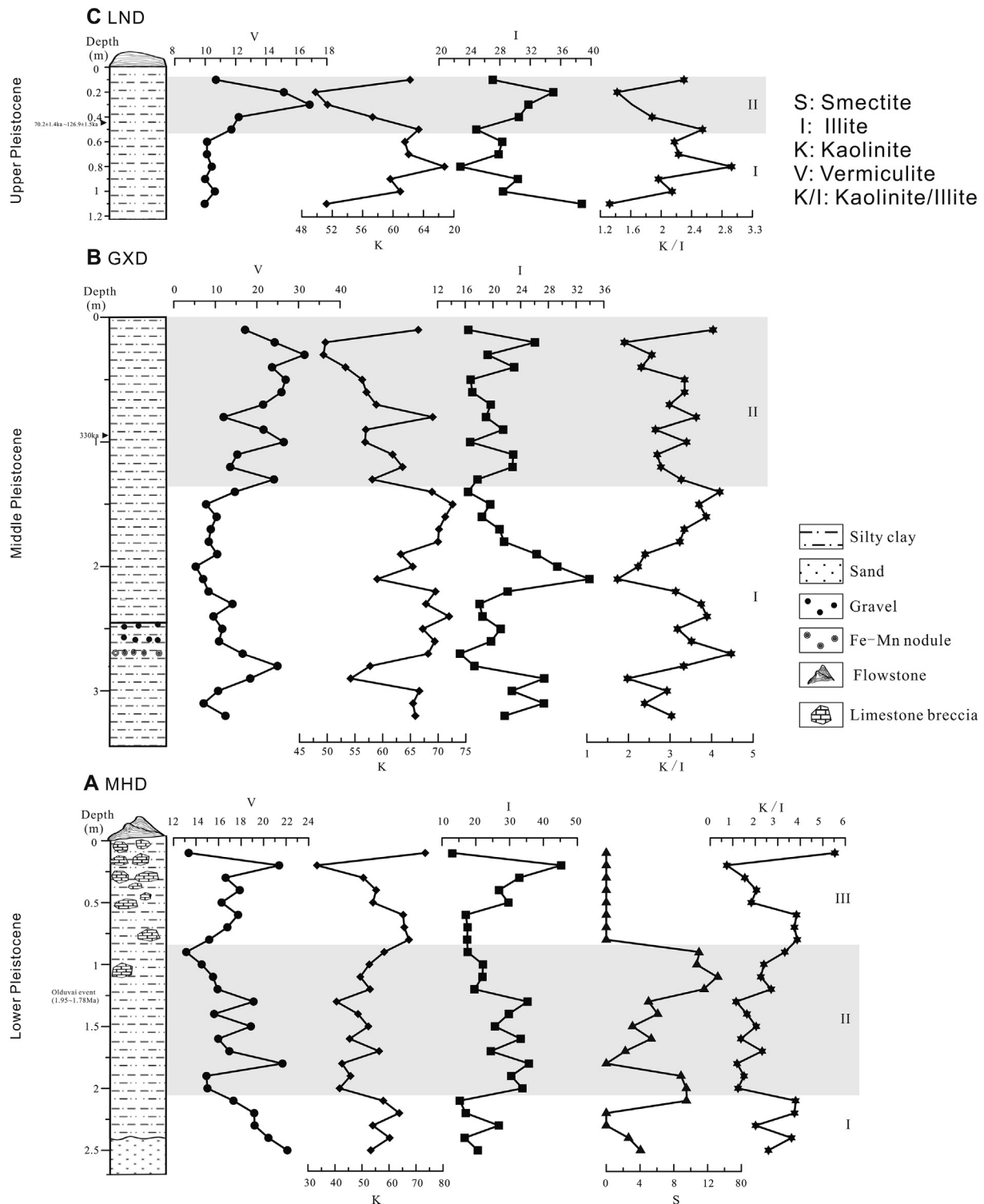


Fig. 8. Paleoclimate reconstruction through clay mineral analyses of profiles from the Early Pleistocene Mohui Cave (a), Middle Pleistocene Ganxian Cave (b), and Late Pleistocene Luna Cave (c). All caves are located in close proximity to each other in the Bubing Basin. Redrawn after Cheng (2016) and Huang (2016).

et al., 2007; Qu et al., 2014; Huang, 2016) is contributing to a better understanding of the environmental framework in which hominins would have appeared, dispersed, and perhaps even gone extinct in the region.

This discussion of hominin fossil distribution across Pleistocene China was necessarily coarse given the variability in the collated data deriving from a wide diversity of sources. However, this database and discussion will hopefully provide the framework in which to investigate

more closely the relationship of hominin dispersals/occupations/extinctions in the face of major climatic changes in the region. In this regard, by having a more robust geochronological dating schematic for many of the sites mentioned here, it may be possible to then combine site occupational histories with paleoclimatic modeling (e.g., Timmermann and Friedrich, 2016), isotope and sediment analyses (Biasatti et al., 2012; Ciner et al., 2015; Huang, 2016; Li et al., 2017, 2017a), and further paleontological study (e.g., Wang et al., 2014; Dong

et al., 2014; Takai et al., 2014; Zhang and Harrison, 2017). By applying this multidisciplinary approach to sites and more broadly, regions that crosscut time periods it could provide more robust information on the nature of these Pleistocene hominin dispersal/occupation/extinction events.

Investigating these questions from different angles is not only important to discussions of modern human origins (Bae et al., 2017a, 2017b), but to examining decision-making by earlier hominins across the region when faced with climatic changes which may have prompted them to simply move, concentrate in various refugia, assimilate with other populations, or possibly even go extinct (Anton, 2007; Dennell, 2009; Bae, 2010; Potts, 2012). In this regard, what is the nature of the evolutionary history of *H. erectus* and mid-Pleistocene *Homo* in the region needs to be more intensively investigated (Bae, 2010). For instance, did *H. erectus* simply evolve into mid-Pleistocene *Homo*? Did mid-Pleistocene *Homo* move into the region and replace *H. erectus*, a so-called “early replacement event” (Groves and Lahr, 1994)? Was there in fact a third major dispersal event out of Africa as postulated by Templeton (2002) during the Middle Pleistocene where some degree of introgression occurred? Importantly, what role did paleoclimatic variation play in these hominin interactions which could have ranged from different populations being forced to meet in refugia to simply going extinct?

4. Conclusions

At the broader Early/Middle/Late Pleistocene level the hominin fossil site distribution data may be informative. Several of the primary observations drawn here are:

1. During the Early and early Middle Pleistocene, with Zhoukoudian Locality 1 being an exception given the more recent dates, hominins were more restricted to central and southern China. This is interesting given that there are reported sites dating as early as 1.66 Ma in the Nihewan Basin, northern China, that despite an absence of *H. erectus* fossils have stone tool collections found in association with vertebrate faunas. Further, the Early Pleistocene *H. erectus* fossils from Dmanisi, Georgia are clearly an early latitudinal appearance.
2. With the appearance of mid-Pleistocene *Homo* during the late Middle Pleistocene, hominin fossils are present in higher, central, and lower latitudes in China.
3. By the advent of the Late Pleistocene, *H. sapiens* are found in higher densities and by the end of MIS 3, human foragers are found well established in higher altitude environments (e.g., Qinghai-Tibetan Plateau), though movement into regions higher than 1000 MASL begins to appear sporadically during the late Middle Pleistocene.

The intent of this paper was to evaluate Pleistocene hominin fossil localities in China from a broad paleoecological approach and raise points that warrant more detailed investigation. Questions remain about whether hominins were restricted to refugia, moved south toward warmer climates, or simply went extinct during glacial periods. Further, what was the nature of the interactions of different Pleistocene hominin groups if and when they met. The observations and questions raised here should serve to lay the foundation from which more detailed analyses may be undertaken of Pleistocene hominin mobility and behavioral strategies in the face of an ever changing climate. The paleoanthropological data in eastern Asia can be better understood if evaluated in concert with paleoclimate data.

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References

- Aldenderfer, M., Zhang, Y.N., 2004. The prehistory of the Tibetan Plateau to the seventh century AD: perspectives and research from China and the West since 1950. *J. World Prehist.* 18, 1–55.
- Ambrose, S.H., 1998. Late Pleistocene human population bottlenecks, volcanic winter, and differentiation of modern humans. *J. Hum. Evol.* 34, 623–651.
- An, Z., Ho, C.K., 1989. New magnetostratigraphic dates of Lantian *Homo erectus*. *Quat. Res.* 32, 213–221.
- Anton, S.C., 2007. Climatic influences on the evolution of early *Homo*? *Folia Primatol.* 78, 365–388.
- Anton, S.C., Swisher, C.C.I.I.I., 2004. Early dispersals of *Homo* from Africa. *Annu. Rev. Anthropol.* 33, 271–296.
- Anton, S.C., Leonard, W.R., Robertson, M.L., 2002. An ecomorphological model of the initial hominid dispersal from Africa. *J. Hum. Evol.* 43, 773–785.
- Bae, C.J., 2010. The late Middle Pleistocene hominin fossil record of eastern Asia: synthesis and review. *Ybk. Phys. Anthropol.* 53, 75–93.
- Bae, C.J., 2014. Pleistocene cave sites in Korea: importance to paleoanthropology? In: Sanz, N. (Ed.), *Human Origin Sites and the World Heritage Convention in Asia*, HEADS 3. UNESCO, Paris, pp. 145–155.
- Bae, C.J., 2017. Late Pleistocene human evolution in eastern Asia: behavioral perspectives. *Curr. Anthropol.* 58, S514–S526.
- Bae, C.J., Wang, W., Zhao, J., Huang, S., Tian, F., Shen, G., 2014. Modern human teeth from Late Pleistocene Luna cave (Guangxi, China). *Quat. Int.* 354, 169–183.
- Bae, C.J., Douka, K., Petraglia, M.D., 2017a. On the origin of modern humans: Asian perspectives. *Science* 358 (6368), eaai9067.
- Bae, C.J., Douka, K., Petraglia, M.D., 2017b. Human colonization of Asia in the late Pleistocene: introduction to supplement 17. *Curr. Anthropol.* 58, S373–S382.
- Beall, C.M., 2001. Adaptations to altitude: a current assessment. *Annu. Rev. Anthropol.* 30, 423–456.
- Beeton, T.A., Glantz, M.M., Trainer, A.K., Temirkbekov, S.S., Reich, R.M., 2014. The fundamental hominin niche in late Pleistocene Central Asia: a preliminary refugium model. *J. Biogeogr.* 41, 95–110.
- Bennett, K.D., Provan, J., 2008. What do we mean by ‘refugia’? *Quat. Sci. Rev.* 27, 2449–2455.
- Biasatti, D., Wang, Y., Gao, F., Xu, Y., Flynn, L., 2012. Paleocologies and paleoclimates of Cenozoic mammals from Southwest China: evidence from stable carbon and oxygen isotopes. *J. Asia Earth Sci.* 44, 48–61 (Special Issue on Asian Climate and Tectonics).
- Boaz, N.T., Ciochon, R.L., Xu, Q., Liu, J., 2004. Mapping and taphonomic analysis of the *Homo erectus* loci at locality 1 Zhoukoudian, China. *J. Hum. Evol.* 46, 519–549.
- Bocherens, H., Schrenk, F., Chaimanee, Y., Kullmer, O., Mörke, D., Pushkina, D., Jaeger, J.J., 2017. Flexibility of diet and habitat in Pleistocene South Asian mammals: implications for the fate of the giant ape *Gigantopithecus*. *Quat. Int.* 434, 148–155.
- Boivin, N., Fuller, D.Q., Dennell, R., Allaby, R., Petraglia, M.D., 2013. Human dispersal across diverse environments of Asia during the upper Pleistocene. *Quat. Int.* 300, 32–47.
- Buzhilova, A., Derevianko, A., Shunkov, M., 2017. The northern dispersal route: bioarchaeological data from the late Pleistocene anthropological of Altai, Siberia. *Curr. Anthropol.* 58, S491–S503.
- Chen, T.M., Zhou, L.P., 2009. Dating of the Peking man site: a comparison between existing chronology and the $^{26}\text{Al}/^{10}\text{Be}$ burial ages. *Acta Antro. Sin.* 28, 285–291 (in Chinese).
- Chen, T.M., Yuan, S.X., Gao, S.J., 1984. The study on uranium-series dating of fossil bones and an absolute age sequence for the main Paleolithic sites of North China. *Acta Antro. Sin.* 3, 259–269 (in Chinese).
- Chen, T.M., Yuan, S.X., Gao, S.J., Hu, Y.Q., 1987. Uranium series dating of fossil bones from Hexian and Chaoxian fossil human sites. *Acta Antro. Sin.* 6, 249–254 (in Chinese).
- Chen, T.M., Qian, Y., En, W., 1994. Antiquity of *Homo sapiens* in China. *Nature* 368, 55–56.
- Chen, T.M., Yang, Q., Hu, Y.Q., Bao, W.B., Li, T.Y., 1997. ESR dating of tooth enamel from Yunxian *Homo erectus* site, China. *Quat. Sci. Rev.* 16, 455–458.
- Chen, G.J., Wang, W., Mo, J.Y., Huang, Z.T., Tian, F., Huang, W.W., 2001. Pleistocene vertebrate fauna from Wuyun cave of Tiandong County, Guangxi. *Vertebrata Palasiatica* 40 (1), 42–51 (in Chinese with English abstract).
- Cheng, L.L., 2016. Distributions and Paleo-Environment Implication of Biomarkers in Sediments from the Mohui Cave in Tiandong, Guangxi Province. China University of Geosciences (Wuhan), MA Thesis.
- Ciner, B., Wang, Y., Deng, T., Flynn, L., Hou, S., Wu, W., 2015. Stable carbon and oxygen isotopic evidence for late Cenozoic environmental change in Northern China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 440, 750–762.
- Ciochon, R., Olsen, J., James, J., 1990. *Other Origins: The Search for the Asian Ape in Human Prehistory*. Bantam Books, New York.
- Conroy, G.C., Pontzer, H., 2012. *Reconstructing Human Origins*, 3rd edition. WW Norton, New York.
- Curnoe, D., Ji, X.P., Herries, A.I., Bai, K.N., Taçon, P.S., Bao, Z.D., Fink, D., Zhu, Y.S., Hellstrom, J., Luo, Y., Cassis, G., Su, B., Wroe, S., Hong, S., Parr, W.C., Huang, S.M., Rogers, N., 2012. Human remains from the Pleistocene–Holocene transition of Southwest China suggest a complex evolutionary history for east Asians. *PLoS One* 7, e31918.
- Demeter, F., Shackelford, L.L., Bacon, A.M., Düringer, P., Westaway, K.,

- Sayayongkhamdy, T., Braga, J., Sichanthongtip, P., Khamdalayong, P., Ponche, J.L., Wang, H., Lundstrom, C., Patole-Edoumba, E., Karpoff, A.M., 2012. Anatomically modern human in Southeast Asia (Laos) by 46 ka. *Proc. Natl. Acad. Sci. U. S. A.* 109, 14375–14380.
- Dennell, R.W., 2009. *The Palaeolithic Settlement of Asia*. Cambridge University Press, Cambridge.
- Dennell, R.W., 2013. Hominins, deserts, and the colonisation and settlement of continental Asia. *Quat. Int.* 300, 13–21.
- Dennell, R.W., 2017. Human colonization of Asia in the late Pleistocene: the history of an invasive species. *Curr. Anthropol.* 58, S383–S396.
- Dennell, R.W., Martín-Torres, M., Bermudez de Castro, J.M., 2011. Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. *Quat. Sci. Rev.* 30, 1511–1524.
- Derevianko, A.P., Rybin, E.P., 2003. The earliest representations of symbolic behavior by Paleolithic humans in the Altai Mountains. *Archaeol. Ethnol. Anthropol. Eurasia* 15, 27–50.
- Dong, W., Liu, J.Y., Zhang, L.M., Xu, Q.Q., 2014. The early Pleistocene water buffalo associated with *Gigantopithecus* from Chongzuo in southern China. *Quat. Int.* 354, 86–93.
- Du, B.P., Zhou, Y., Sun, J.H., Zhang, L.Z., Xia, H.R., Wang, Y.R., Zhao, L.X., 2014. A new discovered human occipital fossil from Shigou Quarry, Xiangfen County, Shanxi Province of North China. *Acta Antrop. Sin.* 33, 437–447 (in Chinese).
- Etlar, D.A., 1996. The fossil evidence for human evolution in Asia. *Annu. Rev. Anthropol.* 25, 275–301.
- Etlar, D.A., Crummett, T.L., Wolpoff, M.H., 2001. Longgupo: early Homo colonizer or late Pliocene *Lufengpithecus* survivor in South China. *J. Hum. Evol.* 16, 1–12.
- Fu, R., Shen, G., He, J., Ren, H., Feng, Y.X., Zhao, J.X., 2008. Modern Homo sapiens skeleton from Qianyang cave in Liaoning, northeastern China and its U-series dating. *Hum. Evol.* 55, 349–352.
- Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher, C.C.I.I.I., Ferring, R., Justus, A., Nioradze, M., Tvalchrelidze, M., Anton, S.C., Bosinski, G., Jöris, O., Lumley, A., Majsuradze, G., Mouskhelishvili, A., 2000. Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: taxonomy, geological setting, and age. *Science* 288, 1019–1025.
- Gao, X., Huang, W., Xu, Z., Ma, Z., Olsen, J.W., 2004. 120–150 ka human tooth and ivory engravings from Xinglongdong cave, three gorges region, South China. *Chin. Sci. Bull.* 49, 175–180.
- Gao, B., Shen, G.J., Ji, X.P., Cheng, H., 2007. U-series dating of Longtanshan cave in Chenggong, Yunnan Province. *Carsologica Sinica* 26, 321–325.
- Glantz, M., Van Arsdale, A., Temirbekov, S., Beeton, T., 2018. How to survive the glacial apocalypse: hominin mobility strategies in late Pleistocene Central Asia. *Quat. Int.* 466 (Part A), 82–92.
- Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W., Fritz, M.H.Y., Hansen, N.F., Durand, E.Y., Malaspina, A.S., Jensen, J.D., Marques-Bonet, T., Alkan, C., Prüfer, K., Meyer, M., Burbano, H.A., Good, J.M., Schultz, R., Aximu-Petri, A., Butto, A., et al., 2010. A draft sequence of the Neanderthal genome. *Science* 328, 710–722.
- Groucutt, H.S., Petraglia, M.D., Bailey, G., Scerri, E.M.L., Parton, A., Clark-Balzan, L., Jennings, R.P., Lewis, L., Blinkhorn, J., Drake, N.A., Breeze, P.S., Inglis, R.H., Devès, M.H., Meredith-Williams, M., Bovin, N., Thomas, M.G., Scally, A., 2015. Rethinking the dispersal of Homo sapiens out of Africa. *Evol. Anthropol.* 24, 149–164.
- Groves, C.P., Lahr, M.M., 1994. A bush not a ladder: speciation and replacement in human evolution. *Perspect. Hum. Biol.* 4, 1–11.
- Grün, R., Huang, P.H., Huang, W., McDermott, F., Thorne, A., Stringer, C.B., Yan, G., 1998. ESR and U-series analyses of teeth from the palaeoanthropological site of Hexian, Anhui province, China. *J. Hum. Evol.* 34, 555–564.
- Han, D.F., Xu, C.H., 1985. Pleistocene mammalian faunas of China. In: Rukang, Wu, Olsen, J.W. (Eds.), *Palaeoanthropology and palaeolithic archaeology in the People's Republic of China*. Academic Press, New York, pp. 267–286.
- Huang, S.M., 2016. Pleistocene Environment Change Recorded by the Deposits of the Caves of Bubing Basin in Guangxi (Ph.D. Dissertation). China University of Geosciences, Wuhan.
- Hublin, J.J., Roebroeks, W., 2009. Ebb and flow or regional extinctions? On the character of Neandertal occupation of northern environments. *C. R. Palevol* 8, 503–509.
- Indriati, E., Swisher III, C.C., Lepre, C., Quinn, R.L., Suriyanto, R.A., Hascaryo, A.T., Grün, R., Feibel, C.S., Pobiner, B.L., Aubert, M., Lees, W., Antón, S.C., 2011. The age of the 20 meter Solo River terrace, Java, Indonesia and the survival of *Homo erectus* in Asia. *PLoS One* 6, e21562.
- Iwamoto, M., Hasegawa, Y., 1972. Two macaque fossil teeth from the Japanese Pleistocene. *Primates* 13, 77–81.
- Jablonski, N.G., 2005. Primate homeland: forests and the evolution of primates during the Tertiary and Quaternary in Asia. *Anthropol. Sci.* 113, 117–122.
- Jablonski, N.G., Whitfort, M.J., Robert-Smith, N., Xu, Q., 2000. The influence of life history and diet on the distribution of catarrhine primates during the Pleistocene in eastern Asia. *J. Hum. Evol.* 39, 131–157.
- Janis, C.M., 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annu. Rev. Ecol. Syst.* 24, 467–500.
- Jaubert, J., 2015. The Paleolithic peopling of Mongolia: An updated assessment. In: Kaifu, Y., Izuhu, M., Goebel, T., Sato, H., Ono, A. (Eds.), *Emergence and Diversity of Modern Human Behavior in Paleolithic Asia*. Texas A&M Press, College Station, Texas, pp. 453–469.
- Jia, L.P., Wei, Q., 1976. Xujiayao Palaeolithic site, in Yanggao County, Shanxi Province. *Archaeology* 2, 97–114 (in Chinese).
- Jin, C., Harrison, T., Dong, W., Bae, C.J., 2014. Multidisciplinary perspectives on the *Gigantopithecus* fauna and Quaternary biostratigraphy in eastern Asia. *Quat. Int.* 354, 1–3.
- Kaifu, Y., 2017. Archaic hominin populations in Asia before the arrival of modern humans: their phylogeny and implications for the “southern Denisovans.”. *Curr. Anthropol.* 58 (suppl. 17), S418–S433.
- Kaifu, Y., Fujita, M., 2012. Fossil record of early modern humans in East Asia. *Quat. Int.* 248, 2–11.
- Kaifu, Y., Aziz, F., Indriati, E., Jacob, T., Kurniawan, I., Baba, H., 2008. Cranial morphology of Javanese *Homo erectus*: new evidence for continuous evolution, specialization, and terminal extinction. *J. Hum. Evol.* 55, 551–580.
- Keates, S.G., Hodgins, G.W., Kuzmin, Y.V., Orlova, L.A., 2007. First direct dating of a presumed Pleistocene hominid from China: AMS radiocarbon age of a femur from the Ordos plateau. *J. Hum. Evol.* 53, 1–5.
- Klein, R.G., 2009. *The Human Career: Human Biological and Cultural Origins*, 3rd ed. University of Chicago Press, Chicago.
- Li, T.Y., Etlar, D.A., 1992. New middle Pleistocene hominid crania from Yunxian in China. *Nature* 357, 404–407.
- Li, H., Wu, X., Li, S., Huang, W., Liu, W., 2010. Late Pleistocene human skull from Jingchuan, Gansu Province. *Chin. Sci. Bull.* 55, 1047–1052.
- Li, Z.T., Xu, Q., Zhang, S.R., Hun, L.Y., Li, M.Y., Xie, F., Wang, F.G., Liu, L.Q., 2014. Study on stratigraphic age, climate changes and environment background of Houjiayao site in Nihewan Basin. *Quat. Int.* 349, 42–48.
- Li, Z.Y., Wu, X.J., Zhou, L.P., Liu, W., Gao, X., Nian, X.M., Trinkaus, E., 2017b. Late Pleistocene archaic human crania from Xuchang, China. *Science* 355, 969–972.
- Li, D.W., Hu, C.Y., Wang, W., Chen, J., Tian, F., Huang, S.M., Bae, C.J., 2017a. Reconstruction of the late Middle Pleistocene paleoecology and paleoenvironment of southern China: evidence from the stable isotope record of quaternary mammalian teeth from Tantang cave, Guangxi. *Quat. Int.* 434, 156–162.
- Li, F., Bae, C.J., Ramsey, C.B., Chen, F.Y., Gao, X., In press. Re-dating Zhoukoudian Upper Cave Northern China. *J. Hum. Evol.*
- Liaoning Museum, Benxi Museum, 1986. Miaohoushan Paleolithic Site in Benxi, Liaoning Province. Cultural Relics Press, Beijing (in Chinese).
- Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records. *Paleoceanography* 20 (1).
- Liu, W., Jin, C.Z., Zhang, Y.Q., Cai, Y.J., Xing, S., Wu, X.J., Chen, H., Edwards, L., Pan, W.S., Qin, D.G., An, Z.S., Trinkaus, E., Wu, X.Z., 2010a. Human remains from Zhirendong, South China, and modern human emergence in East Asia. *Proc. Natl. Acad. Sci. U. S. A.* 107, 19201–19206.
- Liu, W., Wu, X., Pei, S., Wu, X., Norton, C.J., 2010b. Huanglong cave: a Late Pleistocene human fossil site in Hubei Province, China. *Quat. Int.* 211, 29–41.
- Liu, W., Wu, X.J., Xing, S., Zhang, Y.Y., 2014. *Human Fossils in China*. Science Press, Beijing (in Chinese).
- Liu, W., Martín-Torres, M., Cai, Y.J., Xing, S., Tong, H.W., Pei, S.W., Sier, M.J., Wu, X.H., Lawrence, E., Cheng, H., Li, Y.Y., Yang, X.X., de Castro, J.M.B., Wu, X.J., 2015. The earliest unequivocally modern humans in southern China. *Nature* 526, 696–699.
- Lordkipanidze, D., de León, M.S.P., Margvelashvili, A., Rak, Y., Rightmire, G.P., Vekua, A., Zollikofer, C.P.E., 2013. A complete skull from Dmanisi, Georgia, and the evolutionary biology of early Homo. *Science* 342, 326–331.
- Lycett, S.J., Bae, C.J., 2010. The Movius line controversy: the state of the debate. *World Archaeol.* 42 (4), 521–544.
- Madsen, D.B., Ma, H., Brantingham, P.J., Gao, X., Rhode, D., Zhang, H., Olsen, J.W., 2006. The late Upper Paleolithic occupation of the northern Tibetan Plateau margin. *J. Archaeol. Sci.* 33, 1433–1444.
- Michel, V., Valladas, H., Shen, G., Wang, W., Zhao, J.X., Shen, C.C., Valensi, P., Bae, C.J., 2016. The earliest modern Homo sapiens in China? *J. Hum. Evol.* 101, 101–104.
- Mijares, A.S., Detroit, F., Piper, P., Grun, R., Bellwood, P., Aubert, M., Champion, G., Cueva, N., De Leon, A., Dizon, E., 2010. New evidence for a 67,000-year-old human presence at Callao cave, Luzon, Philippines. *J. Hum. Evol.* 59, 123–132.
- Moore, L.G., Niermeyer, S., Zamudio, S., 1998. Human adaptation to high altitude: regional and life-cycle perspectives. *Yrb. Phys. Anthropol.* 41, 25–64.
- Nakazawa, Y., 2017. On the Pleistocene population history in the Japanese archipelago. *Curr. Anthropol.* 58, S539–S552.
- Nakazawa, Y., Bae, C.J., In press. Quaternary paleoenvironmental variation and its impact on initial human dispersals into the Japanese Archipelago, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* <https://doi.org/10.1016/j.palaeo.2017.12.030>.
- Nelson, S.V., 2014. The paleoecology of early Pleistocene *Gigantopithecus blacki* inferred from isotopic analyses. *Am. J. Phys. Anthropol.* 155, 571–578.
- Norton, C.J., 2000. The current state of Korean paleoanthropology. *J. Hum. Evol.* 38, 803–825.
- Norton, C.J., Gao, X., 2008a. Hominin-carnivore interactions during the Chinese early Paleolithic: taphonomic perspectives from Xujiayao. *J. Hum. Evol.* 55, 164–178.
- Norton, C.J., Gao, X., 2008b. Zhoukoudian upper cave revisited. A taphonomic perspective. *Curr. Anthropol.* 49, 732–745.
- Norton, C.J., Jin, J.J.H., 2009. The evolution of modern human behavior in East Asia: current perspectives. *Evol. Anthropol.* 18, 247–260.
- Norton, C.J., Jin, C.Z., Wang, Y., Zhang, Y.Q., 2010a. Rethinking the Palearctic-Oriental Biogeographic Boundary in Quaternary China. In: Norton, C.J., Braun, D. (Eds.), *Asian Paleoanthropology: From Africa to China and Beyond*. Vertebrate Paleobiology and Paleoanthropology Series Springer Press, Dordrecht, The Netherlands, pp. 81–100.
- Norton, C.J., Kondo, Y., Ono, A., Zhang, Y.Q., Diab, M.C., 2010b. The nature of megafaunal extinctions during the MIS 3-2 transition in Japan. *Quat. Int.* 211, 113–122.
- O'Connor, S., Louys, J., Kealy, S., Carro, S.C.S., 2017. Hominin dispersal and settlement east of Huxley's line: the role of sea level changes, island size, and subsistence behavior. *Curr. Anthropol.* 58, S567–S582.
- Pei, W.C., 1939. On the upper cave industry. *Palaeontol. Sin.* 9, 1–58.
- Petraglia, M.D., Korisettar, R., Bovin, N., Clarkson, C., Ditchfield, P., Jones, S., Koshy, J., Lahr, M.M., Oppenheimer, C., Pyle, D., Roberts, R., Schwenninger, J.L., Arnold, L.,

- White, K., 2007. Middle Paleolithic assemblages from the Indian subcontinent before and after the Toba supereruption. *Science* 317, 114–116.
- Petruglia, M.D., Ditchfield, P., Jones, S., Korisettar, R., Pal, J.N., 2012. The Toba volcanic super-eruption, environmental change, and hominin occupation history in India over the last 140,000 years. *Quat. Int.* 258, 119–134.
- Pope, G.G., 1992. Craniofacial evidence for the origin of modern humans in China. *Yrb. Phys. Anthropol.* 35, 243–298.
- Potts, R., 2012. Evolution and environmental change in early human prehistory. *Annu. Rev. Anthropol.* 41, 151–167.
- Qiu, Z.L., Zhang, Y.Y., Hu, S.J., 1985. Human tooth and Paleolithic found at locality 2 of Longtanshan, Chenghong, Kunming. *Acta Antro. Sin.* 4, 233–241 (in Chinese).
- Qu, Y., Jin, C., Zhang, Y., Hu, Y., Shang, X., Wang, C., 2014. Preservation assessments and carbon and oxygen isotopes analysis of tooth enamel of *Gigantopithecus blacki* and contemporary animals from Sanhe cave, Chongzuo, South China during the Early Pleistocene. *Quat. Int.* 354, 52–58.
- Rampino, M.R., Self, S., 1992. Volcanic winter and accelerated glaciation following the Toba super-eruption. *Nature* 359, 50–52.
- Reich, D., Green, R.E., Kircher, M., Krause, J., Patterson, N., Durand, E.Y., Viola, B., Briggs, A.W., Stenzel, U., Johnson, P.L.F., Maricic, T., Good, J.M., Marques-Bonet, T., Alkan, C., Fu, Q., Mallick, S., Li, H., Meyer, M., Eichler, E.E., Stoneking, M., Richards, M., Talamo, S., Shunkov, M.B., Derevianko, A.P., Hublin, J.J., Kelso, J., Slatkin, M., Paabo, S., 2010. Genetic history of an archaic hominin group from Denisova cave in Siberia. *Nature* 468, 1053–1060.
- Rightmire, G.P., 2008. Homo in the middle Pleistocene: hypodigms, variation, and species recognition. *Evol. Anthropol.* 17, 8–21.
- Rink, W.J., Schepartz, L.A., Miller-Antonio, S., Huang, W., Hou, Y., Bakken, D., Richter, D., Lareau, H., 2003. Electron Spin Resonance (ESR) Dating of Mammalian Tooth Enamel at Panxian Dadong Cave, Guizhou, China. In: Shen, C., Keates, S. (Eds.), *Current Research in Chinese Pleistocene Archaeology*, BAR International Series 117, pp. 111–118.
- Rink, W.J., Wang, W., Bekken, D., Jones, H.L., 2008. Geochronology of Ailuropoda-Stegodon fauna and *Gigantopithecus* in Guangxi province, southern China. *Quat. Res.* 69, 377–387.
- Roberts, P., Perera, N., Wedage, O., Deraniyagala, S., Perera, J., Eregama, S., Gledhill, A., Petraglia, M.D., Lee-Thorp, J.A., 2015. Direct evidence for human reliance on rain-forest resources in late Pleistocene Sri Lanka. *Science* 347 (6227), 1246–1249.
- Shang, H., Liu, W., Wu, X., Dong, G., 2006. Upper Pleistocene human scapula from Salawusu, Inner Mongolia, China. *Chin. Sci. Bull.* 51, 2110–2115.
- Shang, H., Tong, H., Zhang, S., Chen, F., Trinkaus, E., 2007. An early modern human from Tianyuan cave, Zhoukoudian, China. *Proc. Natl. Acad. Sci. U. S. A.* 104, 6573–6578.
- Shen, G., Linhong, J., 1991. U-series age of Yanhui cave, the site of Tongzi man. *Acta Antro. Sin.* 10, 65–72 (in Chinese).
- Shen, G.J., Liu, J., Jin, L., 1997. Preliminary results on U-series dating of Panxian Dadong in Guizhou Province, S-W China. *Acta Antro. Sin.* 16, 221–230 (in Chinese).
- Shen, G., Ku, T.L., Cheng, H., Edwards, R.L., Yuan, Z., Wang, Q., 2001a. High-precision U-series dating of locality 1 at Zhoukoudian, China. *J. Hum. Evol.* 41, 679–688.
- Shen, G.J., Wang, W., Wang, Q., Pan, Y., 2001b. U-series dating of hominid site Ganqian cave at Tubo, Lujiang, Guangxi in South China. *Acta Antro. Sin.* 20, 238–244 (in Chinese).
- Shen, G., Wang, W., Wang, Q., Zhao, J., Collerson, K., Zhou, C., Tobias, P., 2002. U-series dating of Liujiang hominid site in Guangxi, southern China. *J. Hum. Evol.* 43, 817–829.
- Shen, G., Cheng, H., Edwards, R.L., 2004. Mass spectrometric U-series dating of new cave at Zhoukoudian, China. *J. Archaeol. Sci.* 31, 337–342.
- Shen, G., Wang, W., Cheng, H., Edwards, R.L., 2007. Mass spectrometric U-series dating of Laibin hominid site in Guangxi, southern China. *J. Archaeol. Sci.* 34, 2109–2114.
- Shen, G., Gao, X., Gao, B., Granger, D.E., 2009. Age of Zhoukoudian *Homo erectus* determined with $^{26}\text{Al}/^{10}\text{Be}$ burial dating. *Nature* 458, 198–200.
- Shen, G., Fang, Y., Bischoff, J.L., Feng, Y.X., Zhao, J.X., 2010. Mass spectrometric U-series dating of the Chaonian hominin site at Yinshan, Eastern China. *Quat. Int.* 211, 24–28.
- Shen, G., Wu, X., Wang, Q., Tu, H., Feng, Y., Zhao, J., 2013. Mass spectrometric U-series dating of Huanglong cave in Hubei Province, Central China: evidence for early presence of modern humans in Eastern Asia. *J. Hum. Evol.* 65, 162–167.
- Shen, G., Tu, H., Xiao, D., Qiu, L., Feng, Y., Zhao, J., 2014. Age of Maba hominin site in southern China: evidence from U-series dating of southern branch cave. *Quat. Geochronol.* 23, 56–62.
- Shikama, T., Ling, C.C., Shimoda, N., Baba, H., 2008. Discovery of fossil *Homo sapiens* from Cho-Chen in Taiwan. *Anthropol. Sci.* 84, 131–138.
- Shipman, P., Walker, A., 1989. The costs of becoming a predator. *J. Hum. Evol.* 18, 373–392.
- Takai, M., Zhang, Y., Kono, R.T., Jin, C., 2014. Changes in the composition of the Pleistocene primate fauna in southern China. *Quat. Int.* 354, 75–85.
- Templeton, A., 2002. Out of Africa again and again. *Nature* 416, 45–51.
- Timmermann, A., Friedrich, T., 2016. Late Pleistocene climate drivers of early human migration. *Nature* 538, 92–95.
- Trinkaus, E., Shang, H., 2008. Anatomical evidence for the antiquity of human footwear: Tianyuan and Sunghir. *J. Archaeol. Sci.* 35, 1928–1933.
- Walker, A., Leakey, R. (Eds.), 1993. *The Nariokotome Homo Erectus Skeleton*. Springer Press, The Netherlands.
- Wang, W., 2009. New discoveries of *Gigantopithecus blacki* teeth from Chufeng cave in the Bubing Basin, Guangxi, South China. *J. Hum. Evol.* 57, 229–240.
- Wang, W., Mo, J., 2004. Human fossil teeth newly discovered in Nanshan cave of Fusui, Guangxi. *Acta Antro. Sin.* 23, 130–137 (in Chinese).
- Wang, W., Potts, R., Hou, Y.M., Chen, Y.F., Wu, H.Y., Yuan, B.Y., Huang, W.W., 2005. Early Pleistocene hominid teeth recovered in Mohui cave in Bubing Basin, Guangxi, South China. *Chin. Sci. Bull.* 50, 2777–2782.
- Wang, W., Potts, R., Yuan, B.Y., Huang, W.W., Chen, H., Edwards, L., Ditchfield, P., 2007. Sequence of mammalian fossils, including hominoid teeth, from the Bubing Basin caves, South China. *J. Hum. Evol.* 52, 370–379.
- Wang, W., Liao, W. Li, D.W., Tian, F., 2014. Early Pleistocene large mammalian fauna associated with *Gigantopithecus* at Mohui cave, Bubing Basin, South China. *Quat. Int.* 354, 122–130.
- Westaway, K.E., Louys, J., Awe, R.D., Morwood, M.J., Price, G.J., Zhao, J.X., Aubert, M., Joannes-Boyau, R., Smith, T.M., Skinner, M.M., Compton, T., Bailey, R.M., van den Bergh, G.D., Vos, J.D., Pike, A.W.G., Stringer, C., Saptomo, E.W., Rizal, Y., Zaim, J., Santoso, W.D., Trihascaryo, A., Kinsley, L., Sulistyanto, B., 2017. An early modern human presence in Sumatra 73,000–63,000 years ago. *Nature* 548, 322–325.
- Wu, X., 2000. Longgupo hominoid mandible belongs to ape. *Acta Antro. Sin.* 19, 1–10 (in Chinese).
- Wu, X., Poirier, F.E., 1995. *Human Evolution in China: A Metric Description of Fossils and a Review of the Sites*. Oxford University Press, Oxford.
- Wu, X., Wu, M., 1985. Early *Homo Sapiens* in China. In: Rukang, W., Olsen, J.W. (Eds.), *Palaeoanthropology and Palaeolithic Archaeology in the People's Republic of China*. Academic Press, New York, pp. 91–106.
- Xie, J., Zhang, Z., Yang, F., 1987. Hominin fossils from Wushan, Gansu Province. *Prehist. Res.* 4, 47–52 (in Chinese).
- Xing, S., Martínón-Torres, M., Bermúdez de Castro, J., Wu, X., Liu, W., 2015. Hominin teeth from the early Late Pleistocene site of Xujiayao, northern China. *Am. J. Phys. Anthropol.* 56, 224–240.
- Xing, S., Guan, Y., O'Hara, M., Cai, H., Wang, X., Gao, X., 2017. Late Pleistocene hominin teeth from Laoya cave, southern China. *Anthropol. Sci.* 125, 129–140. (online, DOI). <https://doi.org/10.1537/ase.170802>.
- Yin, G., Bahain, J.J., Shen, G., Tissoux, H., Falguères, C., Dolo, J.M., Han, F., Shao, Q., 2011. ESR/U-series study of teeth recovered from the palaeoanthropological stratum of the Dali man site (Shaanxi Province, China). *Quat. Geochronol.* 6, 98–105.
- Yuan, S.X., Chen, T.M., Gao, S.J., 1986. Uranium series chronological sequence of some Paleolithic sites in South China. *Acta Antro. Sin.* 5, 179–190 (in Chinese).
- Zhang, Y., Harrison, T., 2017. *Gigantopithecus blacki*: a giant ape from the Pleistocene of Asia revisited. *Am. J. Phys. Anthropol.* 162, 153–177.
- Zhang, X., Shen, G.J., Ji, X.P., 2004. U-series dating on fossil teeth from Xiren cave in Xichou, Yunnan Province. *Acta Antro. Sin.* 23, 88–92 (in Chinese).
- Zhang, L., Shen, G.J., Fu, R.Y., Zhao, J.X., 2007. Preliminary results of the U-series age of Miaohoushan site in Benxi, Liaoning Province. *South. Cult.* 3, 54–57 (in Chinese).
- Zhao, J.X., Hu, K., Collerson, K.D., Xu, H.K., 2001. Thermal ionization mass spectrometry U-series dating of a hominid site near Nanjing, China. *Geology* 29, 27–30.
- Zhao, L.X., Zhang, L.Z., Du, B.P., Nian, X.M., Zheng, Y.W., Zhang, Z.W., Wang, C.B., Wang, X.J., Cai, H.Y., 2016. New discovery of human fossils and associated mammal fauna from Mawokou cave in Bijie, Guizhou Province of southern China. *Acta Antro. Sin.* 35, 24–35 (in Chinese).
- Zhao, M., Shen, G.J., He, J.N., Cao, B., Li, H.C., 2017. AMS ^{14}C dating of the hominin archaeological site Chuandong cave in Guizhou Province, southwestern China. *Quat. Int.* 447, 102–110.
- Zheng, S.H., 2004. *Jianshi Man Site*. Science Press, Beijing (in Chinese).
- Zhou, G.X., 2007. *Bailiandong Culture – A Case Study of the Mesolithic*. Guanxi Science and Technology Press, Nanning (in Chinese).
- Zhu, R.X., Hoffman, K.A., Potts, R., Deng, C.L., Pan, Y.X., Guo, B., et al., 2001. Earliest presence of humans in northeast Asia. *Nature* 413, 413–417.
- Zhu, R.X., Potts, R., Xie, F., Hoffman, K.A., Deng, C.L., Shi, C.D., et al., 2004. New evidence on the earliest human presence at high northern latitudes in northeast Asia. *Nature* 431, 559–562.
- Zhu, R.X., Potts, R., Pan, Y.X., Yao, H.T., Lü, L.Q., Zhao, X., Gao, X., Chen, L.W., Gao, F., Deng, C.L., 2008. Early evidence of the genus *Homo* in East Asia. *J. Hum. Evol.* 55, 1075–1085.
- Zhu, Z.Y., Dennell, R., Huang, W.W., Wu, Y., Rao, Z.G., Qiu, S.F., Xie, J.B., Liu, W., Fu, S.Q., Han, J.W., Zhou, H.Y., Ou Yang, T.P., Li, H.W., 2015. New dating of the *Homo erectus* cranium from Lantian (Gongwangling), China. *J. Hum. Evol.* 78, 144–157.